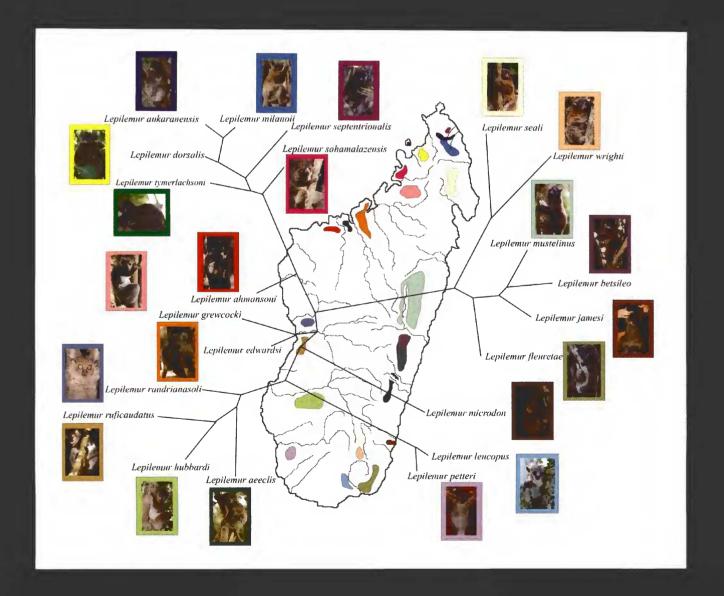


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Molecular and Morphological Analyses of the Sportive Lemurs (Family Megaladapidae: Genus Lepilemur) Reveals 11 Previously Unrecognized Species

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ABSTRACT

Approximately 3,800 base pairs of mitochondrial DNA sequence data (control region or D-loop, 12s ribosomal RNA subunit gene, along with a fragment including a partial segment of cytochrome oxidase subunit III gene to Leucine-tRNA gene) were used to investigate the phylogenetic relationships among the sportive lemurs (Genus *Lepilemur*) and to other lemur genera of Madagascar. The results of our analyses support a monotypic relationship of *Lepilemur* species to other lemur genera, with a sister relationship to the Family Lemuridae. Most importantly, on the basis of both molecular sequence and morphological data, our results show the existence of at least 11 previously unrecognized species of *Lepilemur*. The phylogenetic analyses presented confirm a western/eastern split among the *Lepilemur* species with the exception of the Small-toothed Sportive Lemur found at Ranomafana and Tolongoina, which is included within the western clade. These results underscore the urgency to initiate further detailed studies in previously unstudied sites throughout Madagascar in order to better define lemur species.

Key words: conservation, lemur, *Lepilemur*, phylogeography, systematics

Introduction

Due to its unique species biodiversity and to the continued pressure from human encroachment, Madagascar has been placed at the top of conservation priority lists, or hotspots (Myers 2000). Distributed throughout the island, lemurs are particularly susceptible to extinction risks due to their relatively small fragmented geographic ranges (Jernvall and Wright 1998). All lemurs are protected under the Convention of International Trade of Endangered Species (CITES) and are designated by the IUCN/SSC Red List Categories from critically endangered to threatened depending on the species (IUCN/SSC 1999). Thus, there is a pressing need to understand the taxonomy and phylogeny of lemurs so that a scientifically rational approach to their conservation and management can be developed and implemented.

The taxonomic revision of species and distributions warrants the need to consistently re-evaluate the conservation protection status of lemurs as new information becomes available (Martin 2000). Recent molecular genetic and morphological studies within the genera Avahi, Cheirogaleus, Lepilemur, and Microcebus have led to a significant increase in the number of recognized species (Andriaholinirina et al. 2006; Groves 2000; Kappeler et al. 2005; Louis et al. 2006; Rasoloarison et al. 2000; Thalmann and Geissmann 2005; Zimmermann et al. 1998). Thus, it is critical that we accurately define species and subspecies to better evaluate conservation risks and make appropriate recommendations for the management of wild populations, especially when considering the ranges of newly recognized species of lemurs. The sportive lemurs (Genus *Lepilemur*), a group of strictly nocturnal primates that are superficially indistinguishable with varying degrees of brown, red, white, and gray pelage, are a prime example of species that until now have been largely unrecognized and underrepresented.

The only member of the monotypic Family Megaladapidae, the Genus Lepilemur is currently represented by 11 extant species broadly distributed across Madagascar (Appendix Ib). The taxonomy of the sportive lemurs has been revised several times (Groves 2001; Ishak et al. 1992; Jenkins 1987; Mittermeier et al. 1994; Mittermeier et al. 2006; Montagnon et al. 2001; Petter and Petter-Rousseaux 1960: Petter et al. 1977; Ravaoarimanana 2001; Ravaoarimanana et al. 2004; Rumpler et al. 2001; Rumpler and Albignac 1975; Schwarz 1931; Tattersall 1982; Thalmann 2000; Thalmann and Ganzhorn 2003), most recently by Andriaholinirina et al. (2006) who described three new species. Here, we present further taxonomic revisions by describing 11 new species. We also conducted a phylogenetic analysis of the relationships between these new species and previously recognized ones of the genus Lepilemur.

Although adopting a species description methodology that required a whole voucher has been the

standard, Thalmann and Geissmann (2005) presented an alternative approach through the use of only morphologic data, detailed photographs, and tissue samples. The endangered status of lemurs, all of which have been designated CITES appendix I, along with the digital and molecular technological capabilities of the twenty-first century, can eliminate the immediate requirement of whole vouchers from the wild. Nonetheless, whole vouchers can subsequently supplement the process as they become available opportunistically (e.g., raptor nests or remains of Fossa [Cryptoprocta ferox] predation). Due to the inability to maintain sportive lemurs as long-term live vouchers in captivity, the type series for these newly described *Lepilemur* species are represented by whole blood samples from free-ranging individuals along with a database containing all field data, accessioned sequence data, and photographs. The type series tissues and database are curated at The Museum of Texas Tech University (TK 125501-125566/TTU 104434-104499) (Appendix II).

The database referenced above, as well as additional tables and figures, also are available online at the website of Omaha's Henry Doorly Zoo. See Appendix I for a directory of the appropriate website addresses.

Methods

Sampling.—All lemurs investigated in this study were free-ranging and were immobilized with a CO, projection rifle or blowgun with 10mg/kg of Telazol (Fort Dodge Laboratories, Inc., Ft. Dodge, Iowa; Figure 1; Appendix II). We recorded the location of all immobilized lemurs using a global positioning system (Appendix la). Four 2.0 mm biopsies and 1.0 ec per kilogram of whole blood were collected from each animal and stored in room temperature storage buffer (Longmire et al. 1992). While immobilized, a Home-Again microchip was placed subcutaneously between the scapulas of each lemur (Appendix Ia). This procedure was used to field catalog each animal with a unique recognition code in order to positively re-identify all captured individuals during any future immobilizations. In addition, morphometric measurements were taken.

We present the weight, head crown, body length, and tail length in this publication following the guidelines of Smith and Jungers (1997; Table 1). Also see Appendix Ia, the online Lepilemur Field Data Appendix, for all measurements and e-voucher photographs.

Data Collection.—Genomic DNA was extracted from samples using a phenol-chloroform extraction (Sambrook et al. 1989). From these samples, the following regions of the mitochondrial DNA (mtDNA) were amplified: the displacement loop or control region (D-loop; Baker et al. 1993; Wyner et al. 1999); the 12s subunit ribosomal RNA gene, along with a portion of the tRNA^{Phe} (12s rRNA; Hedges 1994; Wyner et al. 1999); and a fragment of the cytochrome oxidase subunit III gene (COIII); NADH-dehydroge-

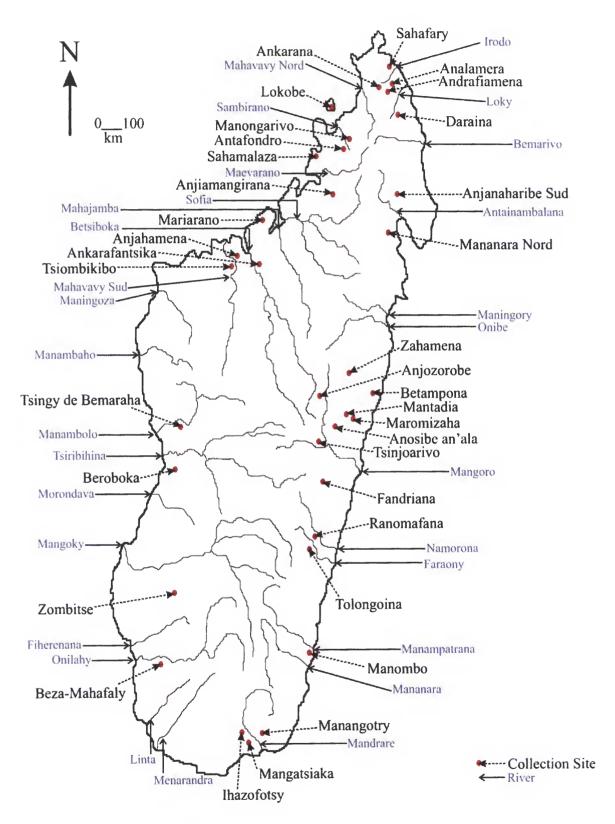


Figure 1. Sample distribution map of the sportive lemurs of Madagascar.

Table 1. Morphometric data collected from sedated individuals. (Individual morphological data available online; see Appendix Ia).

Species Name	Common Name	N	Weight	Head Crown	Body Length	Tail Length
			(kg)	(cm)	(cm)	(cm)
Lepilemur aeeclis	Aeecl's Sportive Lemur	8	0.86 ± 0.17	7.7±1.2	22.4±1.1	25.4±2.1
Lepilemur ahmansoni	Ahmanson's Sportive Lemur	4	0.61 ± 0.15	6.2 ± 1.2	20.6 ± 1.6	23.8 ± 0.7
Lepilemur ankaranensis	Ankarana Sportive Lemur	24	0.79 ± 0.12	7.1 ± 0.9	21.8 ± 2.0	27.3 ± 1.9
Lepilemur betsileo	Betsileo Sportive Lemur		1.15 ± 0.13	7.5 ± 0.3	25.2±0.1	27.7 ± 1.3
Lepitemur dorsalis	Grey-Backed Sportive Lemur		0.73 ± 0.07	7.3 ± 0.4	22.8±1.5	27.5 ± 0.9
Lepilemur edwardsi	Milne-Edwards's Sportive Lemur	11	1.10 ± 0.11	6.7 ± 0.6	26.3 ± 2.7	28.5 ± 2.1
Lepilemur fleuretae	Fleurete's Sportive Lemur	3	0.98 ± 0.16	7.4 ± 0.3	25.5±2.2	30.2 ± 2.1
Lepilemur grewcocki	Grewcock's Sportive Lemur		0.78 ± 0.20	6.2 ± 0.1	24.8 ± 2.1	28.5 ± 1.8
Lepileinur hubbardi	Hubbard's Sportive Lemur		0.99 ± 0.15	7.5 ± 1.2	23.4 ± 1.4	24.0 ± 1.1
Lepilemur jamesi	James' Sportive Lemur		0.78 ± 2.76	8.0 ± 0.3	25.7 ± 1.5	29.7 ± 1.8
Lepilemur leucopus	White-Footed Sportive Lemur	18	0.54 ± 0.09	6.5 ± 0.7	19.6 ± 1.4	24.2 ± 1.2
Lepilemur microdon	Small-Toothed Sportive Lemur		1.19 ± 0.42	10.8 ± 2.3	27.0 ± 2.2	26.8 ± 3.1
Lepilemur milanoii	Daraina or Swimming Sportive Lemur		0.72 ± 0.10	6.4 ± 0.5	21.6 ± 1.7	26.0 ± 1.4
Lepilemur mustelinus	Weasel Sportive Lemur		0.99 ± 0.21	7.9 ± 1.4	25.8 ± 4.0	25.2 ± 2.1
Lepilemur petteri	Petter's Sportive Lemur		0.63 ± 0.05	5.1 ± 0.4	23.2 ± 0.9	23.7 ± 1.4
Lepilemur randrianasoli	Randrianasoli's Sportive Lemur		0.92 ± 0.08	8.2 ± 0.6	24.1 ± 1.7	27.4 ± 1.8
Lepilemur ruficaudatus	Red-Tailed Sportive Lemur		0.86 ± 0.06	6.9 ± 1.0	24.3 ± 3.6	24.2 ± 1.0
Lepilemur sahamalazensis	Sahamalaza's Sportive Lemur		0.70 ± 0.07	6.3 ± 0.1	19.6 ± 0.3	23.7 ± 2.7
Lepilemur seali	Seal's Sportive Lemur		0.95 ± 0.08	7.4 ± 0.9	27.3 ± 1.4	26.3 ± 1.4
Lepilemur septentrionalis	Northern Sportive Lemur		0.58 ± 0.18	8.3 ± 1.1	18.7 ± 1.7	24.8 ± 4.5
Lepilemur tymerlachsoni	Hawk's Sportive Lemur		0.88 ± 0.10	6.5 ± 0.2	23.1±1.5	24.7 ± 2.3
Lepilemur wrighti	Wright's Sportive Lemur		0.95 ± 0.49	8.0 ± 1.3	25.2±3.1	25.5 ± 1.6

nase subunits 3, 4L, and 4 (ND3, ND4L, and ND4); as well as the tRNA^{Gly}, tRNA^{Arg}, tRNA^{His}, tRNA^{Scr}. and partial tRNA^{Leu} genes (subsequently referred to as the PAST fragment; Pastorini et al. 2000). Using 50 nanograms of genomic DNA, the D-loop (555 bp), 12s rRNA (877 bp), and the PAST (2378 bp) fragments were amplified using the following conditions: 94°C for 30s; 47°C for 1 min; 72°C for 5 min for 35 cycles. Since potential nuclear insertions or mitochondrial pseudogenes within the nuclear genome can be amplified inadvertently, we chose to minimize this likelihood by amplifying both mitochondrial DNA regions as intersecting or overlapping segments (Zhang and Hewitt 1996). Consequently, the 12s rRNA fragment was generated from two amplified segments, and the PAST fragment was generated from seven amplified segments. Additionally, to further eliminate amplification of nuclear insertions, a technique that is species independent and both rapid and efficient derived from the degenerate oligonucleotide-primed PCR method (DOP-PCR; Telenius et al. 1992) was used to generate the PCR products. Adapting this LL-DOP-PCR (long products from low quantity), the sequence data was generated for the D-loop fragments, and 12s rRNA and PAST sequence generated from overlapping segments were confirmed. The samples were electrophoresed on a 1.2% agarose gel to verify the PCR product and purified using QlAquick PCR purification kit (Qiagen; Valencia, California).

Using the BigDye terminator cycle sequencing ready reaction kit by Applied Biosystems the sequence was then run on a 7% polyacrylamide gel by an ABI 377 automated sequencer (Applied Biosystems, Inc.; Foster City, California). Four published internal sequencing primers, 12L1, 12L5, 12H2, and 12H3 (Hedges 1994), were utilized to generate the 12sRNA sequence data, and a suite of internal sequencing primers from Pastorini et al. (2000) and Pastorini et al. (2001) were used to generate the PAST fragment. Additionally, PCR and sequencing primers specific for *Lepilemur* were designed for the PAST fragment, and PCR and sequencing primers specific for lemurs were designed for the 12s rRNA and D-Loop fragments

(Appendix Ic). The sequence fragments were aligned to generate a consensus sequence using Sequencher (Gene Corp; Ann Arbor, Michigan), and the consensus sequences were aligned using ClustalX (Thompson et al. 1997). All aligned sequences are available from the first author upon request. All sequences have been deposited in GenBank and the sequence data and information are available from the referenced accession numbers (Appendix II).

Phylogenetic Analysis.—Maximum-parsimony analysis (MP) was performed for the phylogenetic study of the D-loop, 12s rRNA fragment, PAST fragment, and combined (12s rRNA and PAST fragments) sequence data with PAUP* Version 4.0b10 software (Swofford 2001). Heuristic searches were completed using the random addition sequence (1000 replicates) with the tree bisection-reconnection branch swapping routine. Gaps were considered as a fifth character in MP analyses, but were treated as missing data in the neighbor-joining analyses (NJ). Bootstrap analyses were accomplished with 1500, 1000, 2500, and 1000 pseudoreplicates with the D-loop, 12s rRNA, PAST, and combined data sets, respectively. Only nodes with greater than 50% support were reported. The maximum likelihood (ML) analyses were performed using the program DNAML in PHYLIP 3.65 package (Felsenstein 2005). Due to the large number of taxa and characters and the resulting computational intensity, we pruned the combined sequence dataset by choosing taxa from distinct clades supported in an initial NJ (Saitou and Nei 1987) analysis. The NJ analysis was performed with MEGA 3.1 (Kumar et al. 1993) using Tamura and Nei (1993) gamma distances with an α -parameter value = 0.5, which was estimated using the Yang and Kumar (1996) method; the reliability of internal branches was assessed with 1,500 bootstrap pseudoreplicates. The taxa chosen from the NJ tree for the ML analysis included 55 taxa; RANO229, a Greater Dwarf Lemur [Cheirogaleus major], was used as the outgroup taxon. The ML analysis of these taxa was performed using F84 gamma distances with an α -parameter value = 0.5. The reliability of the internal branches was assessed with 1,000 bootstrap pseudoreplicates.

Bayesians inference analyses were conducted using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The model of evolution was selected by using MrModeltest 2.2, a modified version of Modeltest 3.6 (Nylander 2004; Posada and Crandall 1998). A Markov Chain Monte Carlo (MCMC) run with four simultaneous chains and 1,000,000 generations was performed. The pattern of sequence evolution was estimated by conducting a minimum spanning network generated with the program NETWORK version 4.11 (Bandelt et al. 1999: Forster et al. 2001; Gonzales et al. 1998) and Arlequin, version 2.0 (Schneider et al. 2000). We also conducted Message Passing Clustering (MPC) (Geng et al. 2004. 2005). MPC is an agglomerative, object-oriented clustering algorithm that preserves the clustering process in a tree structure by employing the concept of message passing to describe parallel and spontaneous biological processes, such as speciation. The Kimura (1980) two-parameter nucleotide distances of the 211 Lepilemur samples were used as input for the MPC analysis. These distances were generated using PAUP* version 4.0b10 (Swofford 2001).

In addition to character-based phylogenetic analysis of DNA sequences, PAUP* software (Swofford 2001) was also used to calculate uncorrected pairwise distances for 12s rRNA, ND3, ND4L, ND4, PAST fragment, and 12s rRNA and PAST combined fragments ('p'). As described in Davis and Nixon (1992), Louis et al. (2006), Mayor et al. (2004), and Wyner et al. (1999), we utilized MacClade 3.01 (Maddison and Maddison 1992) and MEGA version 2.0 (Kumar et al. 1993) in a diagnostic search to designate evolutionarily significant units (ESU) using population aggregate analysis (PAA) of the D-loop (544 bp), 12s rRNA (877 bp), and PAST (2378 bp) sequence data for *Lepilemur*. With the sequential addition of each individual without an a priori species designation, a PAA distinguishes attributes or apomorphic characters according to the smallest definable unit (Davis and Nixon 1992; Louis et al. 2006; Mayor et al. 2004).

RESULTS

Mitochondrial DNA sequence data was completed for three fragments, D-loop, 12s rRNA, and PAST fragment (approximately 3800 bp), for 211 individuals, representing all eleven recognized species of sportive lemurs from a total of forty-one sites (Figure 1; Appendix II). All new mtDNA sequences generated for this study were deposited in GenBank and can be acquired through the accession number (Appendix II). The sequence alignments for the data sets are available from the first author upon request. The 12s rRNA fragment consists of the 3' end of the phenylalanine tRNA (22 bp) and a partial section of the 12s rRNA subunit gene (855 bp; Appendix Ig). The PAST fragment consists of the 3' end of the COIII gene (30 bp), the complete NADH-dehydrogenase subunits ND3 (348 bp), ND4L (297 bp), and ND4 (1378 bp), along with the tRNA genes, glycine (73 bp), arginine (73 bp), histidine (70 bp), serine (65 bp), and the 5' portion of leucine (47 bp; Appendix Ig). The polyadenylation of COIII and ND4 genes, insertion of base pairs between ingroup/outgroup comparisons, and other alignment characteristics between lemurs and Homo are consistent with Pastorini et al. (2000).

Based on the phylogenetic inferences of the NJ, MP, and ML analyses of four sequence alignments (D-loop, 12s rRNA, PAST, and 12sRNA-PAST fragment combined), three major Lepilemur subgroups are represented, differentiating the eleven recognized sportive lemur species (Figures 2-4, 6-7; additional figures are available at http://www.omahazoo.com). The first subgroup corresponds to the eastern sportive lemurs, L. mustelinus and L. microdon (the distribution of L. mustelinus and L. microdon is based on Andriaholinirina et al. (2006) and Mittermeier et al. (2006); Appendix Ib). The second subgroup includes the western and southern sportive lemurs, L. edwardsi, L. aeeclis, L. randrianasoli, L. ruficaudatus, and L. leucopus, respectively. The remaining subgroup consists of the recognized northern sportive lemurs, L. septentrionalis, L. ankaranensis, L. dorsalis, and L. sahamalazensis. There is high bootstrap support for the MP and NJ analysis with respect to the topology of the genera and species (Figure 2). In order to verify that our samples are indicative of the three newly described species in Andriaholinirina et al. (2006), we used GenBank to BLAST cytochrome B subunit gene sequence generated for our data set. This confirmed that our samples are representative of those species (GenBank Accession DQ529452-DQ529459; Andriaholinirina et al. 2006). Additionally, 11 distinct subpopulations were identified within the currently recognized Lepilemur species distribution. Each subpopulation is geographically defined by rivers which isolate them by acting as barriers to the recognized species. The results from the population aggregate analysis of the D-loop, 12s rRNA, and PAST sequence data are presented in Tables 2A-C and 3A-C, respectively (the complete diagnosis from the PAA for the D-loop, 12s rRNA, and PAST sequence data are available online; see Appendix Ie). Multiple diagnostic characters define each Lepilemur species, along with the 11 newly described species (Tables 2 and 3). A review of the morphometric data for the 22 species of sportive lemurs is presented in Table 1 (detailed morphological measurements of the individual animals are available online; see Appendix Ia). The complete uncorrected 'p' distance and the Kimura two-parameter distance measures are presented in Appendix Id.

The MP, Bayesian, and MPC analyses are presented in Figures 2 and 3 (also see Appendices Ih and Ii). All analyses differentiate 22 Lepilemur species, including 11 new species. The minimum spanning network presents diagrammatically the speciation among the 22 sportive lemurs (Figure 5). The ML tree was estimated from the combined 12s rRNA/PAST alignment from a subset representing the haplotypes within the data set, and corresponds to the other phylogenetic inferred trees (Figure 7). There is high bootstrap support for the ML analysis with respect to the topology of the genera and species. Specific resolution of sportive lemurs based on phylogenetic inference parallels geographic separation into western, eastern, and northern groups with the exception of L. microdon which is aligned with the western group.

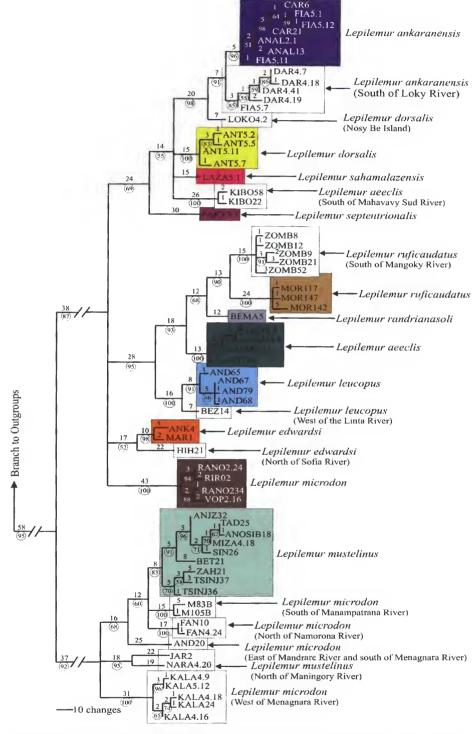


Figure 2. Neighbor-joining phylogram derived fom D-loop DNA sequence data from 67 haplotypes from the 211 *Lepilemur* individuals. Species designated according to the distribution in the current literature (Andriaholinirina et al. 2006; Mittermeier et al. 2006; Appendix Ib). Values above branches indicate number of changes between nodes. Values below branches indicate support of bootstrap pseudoreplicates. Length = 1,698; CI = 0.4346; RI = 0.8299; RC = 0.3607; HI = 0.5811.

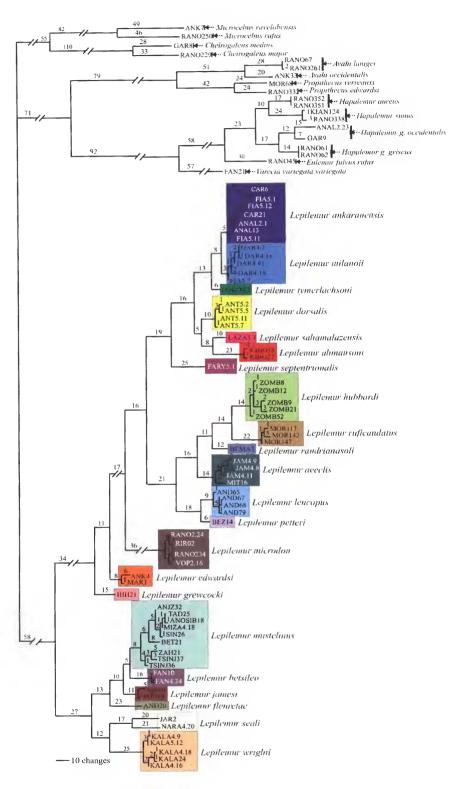


Figure 3. Phylogeny derived from D-loop fragment sequence data from 67 *Lepilemur* haplotypes (one of 80 most parsimonious trees). Values above branches indicate number of changes between nodes.

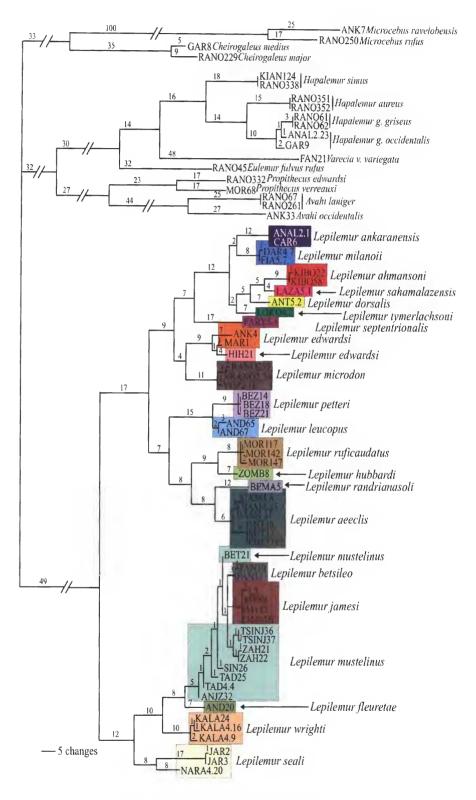


Figure 4. Phylogeny derived from combined 12s rRNA fragment sequence data from 54 haplotypes from 211 *Lepilemur* individuals (one of 128 most parsimonious trees). Values above branches indicate number of changes between nodes. Length = 1,080; C1 = 0.5139; RI = 0.8629; RC = 0.4434; HI = 0.5132.

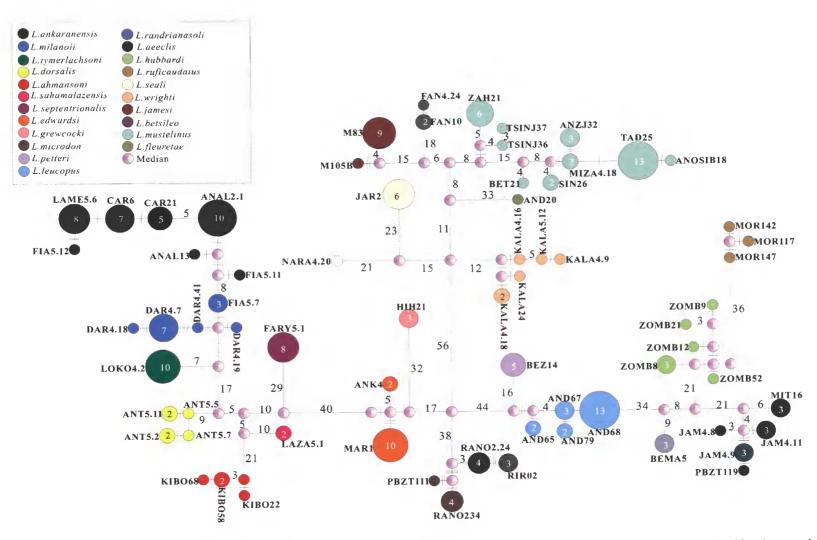


Figure 5. Minimum spanning network of *Lepilemur* haplotypes calculated using Arlequin Version 2 and Network Version 4.11. Identification numbers denote haplotypes corresponding to Appendix II. The minimum number of mutational steps separating matriarchal lines is indicated. Nucleotide substitutions are indicated by dashes. The number of nucleotide differences in their connecting lines (more than 10) is indicated when they are more than one. Missing intermediates are indicated by gray circles. The size of circles approximates the number of individuals with matching haplotypes (circles without any number represent one individual).

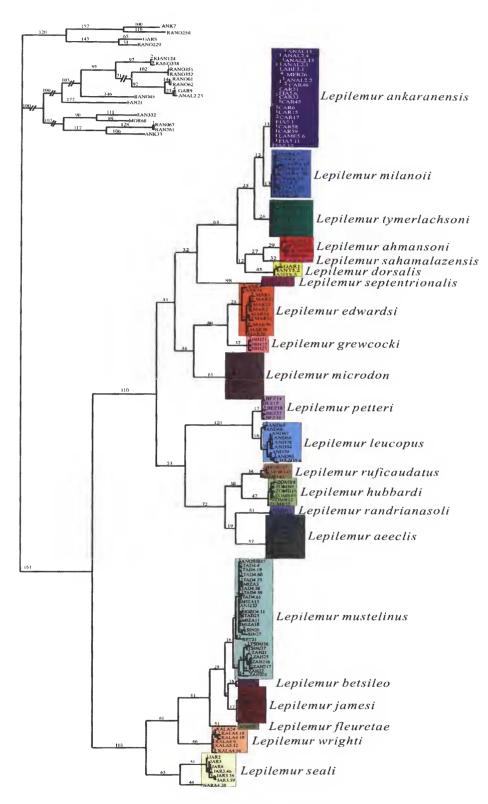


Figure 6. Neighbor-joining phylogram derived from PAST fragment sequence data from 211 *Lepilemur* individuals, representing 156 haplotypes (the phylogram presented maintains branch lengths proportional to the number of changes).

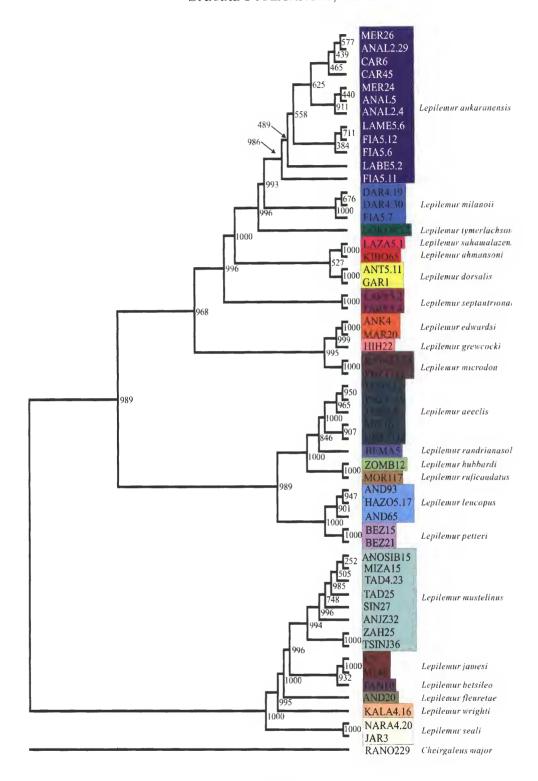


Figure 7. Maximum-likelihood phylogram derived from combined 12s rRNA and PAST fragment sequence data from 55 *Lepilemur* individuals. The phylogram presented with support of 1000 bootstrap pseudoreplicates (values specified on the nodes).

Table 2A. Diagnostic nucleotide sites from the D-loop Pairwise Aggregate Analysis (PAA) of Lepilemur.

	1111111111111111111111122222222222333333
	111223333344445555590001111122222223333399114456778889000115889793335
	1089152347834670457893470347901345691456838280718014569018255784413452
ANAL2.1	CTCAACGCTATTAAAAACCTTCCTGGAGC-ACCCAATTGCAACATTTTTAAATCACCTCAAAACI
DAR4.7	TGG.
LOKO4.2	T
FRAY5.01	TC.G.C-CCTA
ANT5.2	TA
LAZA5.1	TA.CTAAG,CTTA
BEZ14	A~CTAT-TTTTCTA
AND65	GTGTG
MOR117	CC-CGAGGCGGTCCGCTAAGC
ZOMB8	
BEMA5	ATAC-CGTAACCGGCTA.CC
MAR1	ACATC-CCCAAGCCCC
HIH21	ACATC-CCAAGCCTG
KIBO22	TA
JAM4.2°/	G.A.CC-CCATGGTACG.TA
TAD25	TAAC.CA.C.AACCATAAC.GGCA.TCTACATCACT
M83B	, FAAC.CA.C.AACCAFCAAC.AGCATTACT.AACT
FAN10	T.AC.CA.C.AACCATCAAC.GAGCA.TCTCCGCAACT
AND20	.CAACGCA.CGAACCACAGC.GGCTACG.CAGAACT
RANO234	AA.G.CACC-CTJTG.TCTATA
KALA24	TAACA.C.TCACCG.TCCTAAGGTA.TTCTCT.GATC.C
JAR2	T.TTAC.CA.C.AGCCTACCT.GT.GGTCAAACTAAACT

Table 2B. Diagnostic nucleotide sites from the 12s rRNA Pairwise Aggregate Analysis (PAA) of Lepilemur.

	Angeregate Amarysis (1711) by Elephonia.
	1112222233333334444444555566667777777778
	156614534479134468991133689035746892455666895
	6830608450204040999143823988066916433607168664
ANAL5	AAGACTCTAACAAGAATCCCGTAAAATATAAACAACAACACCCGGT
DAR4.7	
LOKO4.2	
FARY5.1	.G.G.G.CG
ANT5.2	TT
LAZA5.1	T
BEZ14	
AND65	TC.G
MORI17	
ZOMB8	
вема5	TTA.TG, C.GC
MARl	T
HIH21	т
KIBO22	T.TG.TG
JAM4,27	C.GC
TAD25	CC.TA
M83B	CTC
FAN10	CC
AND20	C.A.,C
RANO234	T.GG
KALA24	C,CA
JAR2	GTCA

Table 2C. Diagnostic nucleotide sites from the PAST Pairwise Aggregate Analysis (PAA) of Lepilemur.

	11111111111111112222233333333333333333
ANAL5	CCCCAC-AATCCACGAGUTAACAGCCAACACCCAA1GATCCCATACACCACACACACAACAATACGTAATGACCCAACCCAACAATAATTCTCAAAAACTCATAAACAACGCTCACGA
DAR4.7	T. A.
LOK04.2	A T B
FARY5.1	GATGCGG.A1T.GATATATA
ANT5.2	
LAZA5.1	
BEZ14	.TTATA
AND65	.TT
MOR117	GACGAAGCTG
ZOMB8	TCTAGGGTGGGCAAAAA
BEMA5	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$
MAR1	
HIH21	TCGT.GAAAGGG
KIBO22	T
JAM4.27	TC
TAD25	T. T-T. T. A. T. A. C. T. A. T
M83B	T.TA.C.AA.CA.T.A.T.A.T.A.T.A.T.A.
FAN10	G.T. T- T. A. T. A
AND20	. IT I C. T
RAN0234	
KALA24	GT~ T.A C A
JAR2	ATTGTATAGAT.A

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ANALS DAR4.7 LOKO4.2 FARY5.1	ACATAAACCTAACAACCACCCCCAAAAACCCAAACCAAACCAAACCAAAA
ANDS.2 REZI4 NDG5 NOR117	C C C C C C C C C C C C C C C C C C C
EMA5 BR1 IH21 TB022	
TADES M83B FAN10 AND20 RANO234 KALA24 JAR2	

Table 3A. Summary of Population Aggregate Analysis (PAA) D-Loop diagnostic sites for Lepilemur species. Refer to Table 2A. *No Character or Attribute is available for this fragment.

Species	Fragment Size (bp)	PAA base pair location
Lepilemur ankaranensis	540	*
Lepilemur milanoii	540	129
Lepilemur tymerlachsoni	538	117, 301
Lepilemur septentrionalis	536	43, 46, 99, 113, 114, 247
Lepilemur dorsalis	540	534, 535
Lepilemur sahamalazensis	542	*
Lepilemur petteri	534	*
Lepilemur leucopus	535	19
Lepilemur ruficandatus	535	103, 126, 247, 308, 533
Lepilemur hubbardi	535	240, 251, 268, 300
Lepilemur randrianasoli	538	33, 38, 270
Lepileniur edwardsi	545-546	137
Lepilemur grewcocki	544	137, 193, 355
Lepilemur ahmansoni	542	*
Lepilemur aeeclis	537-538	21, 271
Lepilemur mustelinus	552-553	387, 388
Lepilemur jamesi	552	131
Lepilemur betsileo	553	134, 270, 271, 284
Lepilemur fleuretae	550	10, 37, 47, 198, 285, 286, 312, 315
Lepilemur microdon	530 394, 552	25, 34, 44, 57, 107, 110, 119, 120, 121, 123, 124, 125, 135, 136, 137,
Lepilemur wrighti	551	50, 54, 55, 58, 299, 474, 491
Lepilemur sealı	550	1, 18, 32, 54, 104, 126, 212, 218, 300

Table 3B. Summary of Population Aggregate Analysis (PAA) 12s rRNA diagnostic sites for Lepilemur species. Refer to Table 2B. *No Character or Attribute is available for this fragment.

Species	Fragment Size (bp)	PAA base pair location
Lepilemur ankaranensis	855	*
Lepilemur milanoii	855	498
Lepilemur tymerlachsoni	855	394, 693, 854
Lepilemur septentrionalis	855	18, 60, 110, 154, 334, 433, 488
Lepilemur dorsalis	855	761, 796
Lepilemur sahamalazensis	855	294, 766
Lepilemur petteri	855	240
Lepilemur leucopus	855	*
Lepilemur ruficandatus	855	433
Lepilemur hubbardi	855	340
Lepilemur randrianasoli	855	6, 242, 369, 391, 418, 666
Lepilemur edwardsi	854	*
Lepilemur grewcocki	854	*
Lepilemur ahmansoni	855	413, 641, 723, 750, 768
Lepilemin aeeclis	855	389, 556
Lepileum mustelinus	854	*
Lepilemur jamesi	854	66
Lepilemur betsileo	853	434
Lepilemur fleuretae	854	53, 500, 757
Lepilemur microdon	855	148, 235, 270, 757, 786
Lepilemur wrighti	854	349, 746
Lepilemur seali	855	6, 310, 469, 536, 579, 684

Table 3C. Summary of Population Aggregate Analysis (PAA) 12s rRNA diagnostic sites for Lepilemur species. Refer to Table 2C. *No Character or Attribute is available for this fragment.

Species	Fragment Size (bp)	PAA base pair location
Lepilemur ankaranensis	2359-2360	364, 858, 1804
Lepilemur milanoii	2359	342, 769, 1896
Lepilemur tymerlachsoni	2359	152, 328, 1309, 1378, 1456, 1861, 1898, 1995
Lepilemur septentrionalis	2361	44, 113, 211, 214, 274, 353, 354, 533, 551, 555, 576, 674, 734, 1103, 1174, 1231, 1347, 1399, 1448, 1550, 1603, 1777, 2144, 2146, 2366
Lepilemur dorsalis	2361	579, 717, 746, 1507, 1525, 1780, 2163, 2168, 2177, 2236
Lepilemur sahamalazensis	2360	399, 539, 737, 749, 770, 803, 1358
Lepilemur petteri	2360	337, 578, 779, 957, 1615
Lepilemur leucopus	2360-2361	220, 448, 719, 836, 1960
Lepilemur ruficaudatus	2360	94, 127, 365, 667, 776, 919, 1074, 1370, 1783, 1835, 1921, 2068
Lepilemur hubbardi	2361 2245	350, 543, 566, 629, 681, 1015, 1240, 1396, 1559, 1906, 1907, 2111,
Lepilemur randrianasoli	2360	195, 397, 699, 849, 923, 1018, 1035, 1053, 1432, 1444, 1753, 1981, 1988, 2251
Lepilemur edwardsi	2360	856, 1108, 1194, 1343, 1474, 1979
Lepilemur grewcocki	2360	244, 274, 406, 629, 888, 896, 988, 1114, 1226, 1354, 1537, 2130
Lepilemur ahmansoni	2360	46, 304, 350, 1096, 1097, 1285, 1402, 1818, 2141, 2170
Lepilemır aeeclis	2360	535, 548, 563, 581, 761, 975, 1357, 1368, 1423, 1442, 1480, 1990, 2089, 2107
Lepilemur mustelinus	2359-2360	85
Lepilemur jamesi	2360	140, 716, 2144
Lepilemur betsileo	2360	8, 1057
Lepilemur fleuretae	2360 2023	29, 103, 269, 358, 533, 534, 546, 553, 664, 905, 1124, 1574, 2013,
Lepilemur microdon	2361	146, 510, 581, 596, 826, 829, 1171, 1369, 1708, 1954, 1991
Lepilemur wrighti	2360	55, 133, 663, 696, 886, 871, 907, 942, 1105, 1117, 1120, 1294, 1837, 1856, 1936, 2041, 2096
Lepilemur seali	2361	83, 84, 131, 166, 170, 187, 331, 409, 505, 558, 572, 615, 695, 853, 917, 937, 1045, 1228, 1235, 1270, 1332, 1348, 1421, 1423, 1453, 1548, 1795, 1921, 1939, 2056, 2153, 2178, 2179, 2296

DISCUSSION

The persistent and rapid loss of habitat and the resulting fragmentation of panmictic populations have compelled wildlife and conservation agencies to take protective action according to existing guidelines and information with the ultimate goal of prioritizing species and/or sites. The explosive rate of the deforestation in Madagascar, however, has eliminated many of the available options. Because haplotypes can be unique to each population, simply preserving one population will not necessarily maintain species-wide genetic variability. The extinction of any remnant population may not diminish the between-population variance, but may result in the permanent loss of non-neutral alleles from the composite gene pool. The loss can potentially have deleterious effects with the loss of genetic diversity

especially in primates (Pope 1996). Even if the loss of genetic diversity in primates is characterized by an overall loss of heterozygosity with most of the variation found between populations and/or social groups, the genetic loss is dependent on the proportion of the gamete pool contributed by each generation and by lineage effects (Pope 1996). The management of fragmented populations is further complicated by a lack of information, such as full extent of species distribution, from existing populations, and by the mating system and social structure of each species. Therefore, it is important to maintain the composite genetic diversity and the species reservoirs within and among these fragmented habitats.

Historically, sympatric reproductive isolation, as described in the Biological Species Concept (BSC), has been the predominant defining criteria of species status (Mayr 1942). Unfortunately, this concept is difficult to implement or delineate when the putative species in question is a geographically isolated or allopatrically defined population. In this paper, the current Lepilemur taxonomy was examined according to the Phylogenetic Species Concept (PSC) sensu Wheeler and Platnick et al. (2000), Louis et al. (2006), and Mayor et al. (2004). The diagnostic characters or attributes define evolutionarily significant units (ESUs). Several authors suggest that ESUs are equivalent to species as determined through the Phylogenetic Species Concept (Amato et al. 1998; Barrowclough and Flesness 1996; Cracraft 1983). The identification of eleven new species in the following descriptions establishes the essential need for extensive as well as detailed sample collections across Madagascar to determine geographic ranges for all of the sportive lemurs. The constant addition of samples to the PAA data set will continue to test the distinction of these characters.

Due to the inability to maintain sportive lemurs as long-term live vouchers in captivity, whole blood, morphometric, and e-voucher photos will serve as the type series for several of the newly described species. In each case, an attempt was also made to identify existing museum specimens to represent the type series and was listed in that section.

Lepilemur ahmansoni, New Species

Type Series.—Whole blood for KIBO22 (TK125529/TTU104462), adult male; KIBO58 (TK125530/TTU104463), adult female; and KIBO65 (TK125531/TTU104464), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. KIBO22, KIBO58, and KIBO65 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantompohavana, and John R. Zaonarivelo on 23 October 2003, 27 October 2003, and 29 October 2003, respectively.

Type Locality.—MADAGASCAR, Province de Mahajanga, Tsiombikibo Classified Forest, 16°02'24.7"S, 045°48'10.6"E, and northwest of the Mahavavy River.

Description.—L. ahmansoni is a smaller sized sportive lemur (0.61 kg) compared to L. aeeclis (0.86 kg) with a pelage that is primarily dark gray on the body and diffuse reddish-brown on the dorsal surface of the extremities, especially distally. They have similar color patterns to L. aeeclis except L. ahmansoni lacks the prominent dorsal stripe on the dorsal midline of the back as described for L. aeeclis (Andriaholinirina et al. 2006). A diffuse black stripe can be present on the dorsum of the head. The ventrum is dark gray towards the midline but diffuses to a light gray ventrolaterally. The tail is primarily reddish brown, darker on the dorsal surface than the ventral portion which is a light grayish blonde.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, L. ahmansoni differs from the closest relative, L. sahamalazensis, by $5.5\%\pm1\%$ (33 informative sites), $1.6\%\pm0.4\%$ (13 informative sites), and $2.7\%\pm0.3\%$ (70 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, L. ahmansoni differs from the closest species relative to geographic distance, L. aeeclis, by $9.6\%\pm1.3\%$ (69 informative sites), $6.5\%\pm0.8\%$ (59 informative sites), and $11.7\%\pm0.6\%$ (282 informative sites), respectively.

Distribution.—L. ahmansoni is currently known from the Tsiombikibo region, northwest of the Mahavavy River. The southern extent of *L. ahmansoni* is unknown. Further work needs to be conducted to determine if the Maningoza, Manambaho, or Manambolo River is the southern range of *L. ahmansoni* and the northern range of *L. randrianasoli*.

Comparisons and Remarks.—L. ahmansoni is smaller in size than L. ruficaudatus, L. aeeclis, L. randrianasoli, and L. edwardsi (Table 1). Both KIBO58 and KIBO65 were adult females, supporting offspring. Although L. ahmansoni is located geographically closer to L. aeeclis and L. edwardsi, L. ahmansoni is taxonomically closer to the northwest sportive lemurs, L. sahamalazensis and L. dorsalis (Figures 2-6; each species is depicted by specific color throughout the fig-

ures). Additional survey work is required to determine the southern range of *L. ahmansoni* and the northern extent of *L. randrianasoli*. The molecular analysis presented in this paper corroborates the phylogeographic study of Pastorini et al. (2003) and Andriaholinirina et al. (2006), with the Betsiboka River forming the southern limit of *L. edwardsi*. Further studies should be conducted north of Ankarafantsika National Park to determine the northern extent of *L. edwardsi*.

Etymology.—The name ahmansoni is proposed in honor of Robert Ahmanson and the Ahmanson Foundation who have given extensive support to the graduate programs of the Malagasy students in Madagascar and at the Henry Doorly Zoo's Center for Conservation and Research.

Vernacular Names.—Ahmanson's Sportive Lemur.

Lepilemur betsileo, New Species

Type Series.--Whole Blood for FAN11 (TK 125513/TTU104446), adult female; and FAN4.24 (TK125514/TTU104447), adult male are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. FAN11 and FAN4.24 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantompohavana, and John R. Zaonarivelo on 28 October 2000 and 2 April 2004, respectively. According to Jenkins (1987), a specimen, ZD.1981.759 (skin and skull), is held at the British Museum of Natural History from the Ambohimitombo Forest (20°43'S, 047°26'E), which is located within the tentative range of L. betsileo.

Type Locality.— MADAGASCAR, Province de Fianarantsoa, Fandriana Classified Forest, (approximately 20°23'40.5"S, 047°38'06.6"E), and on the Mananjary River.

Description.—This sportive lemur is relatively large (1.11 kg) with a predominantly grayish to reddish brown color pattern. The overall pelage is a mixture

of dark to light gray and reddish brown fur, darker dorsally than ventrally. The pelage is noticeably lighter within the ear pinna bordered by dark brown to black fur along the outer edge of the anterior aspect of the pinna. The anterior portion of the mandible is white in color with the rest of the face gray in color. The tail contrasts sharply with the rest of the body, being black in color.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, L. betsileo differs from its closest relatives by both genetic and geographic distance, L. mustelinus and L. microdon, by $5.2\%\pm0.9\%$ (42 informative sites) and $11.5\%\pm1.3\%$ (76 informative sites), $0.7\%\pm0.2\%$ (9 informative sites) and $6.8\%\pm0.8\%$ (60 informative sites), and $2.2\%\pm0.2\%$ (67 informative sites) and $15.7\%\pm0.8\%$ (370 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, L. betsileo differs from another new species, L. jamesi, by $5.8\%\pm1\%$ (34 informative sites), $1\%\pm0.3\%$ (8 informative sites), and $1.8\%\pm0.2\%$ (41 informative sites), respectively.

Distribution.—L. betsileo is currently known from the Fandriana region, between the Mangoro and Namorona Rivers. The southern and northern distribution of *L. betsileo* is unknown and further work needs to be conducted to confirm the extent of its range.

Comparisons and Remarks.—L. betsileo is intermediate in size to L. mustelinus and L. microdon (Table 1). FAN11 was an adult female, supporting an offspring. L. betsileo is located geographically closest to L. microdon to the southeast and L. mustelinus to the north (Figures 2-6). Additional survey work is required to confirm the southern and northern ranges of L. betsileo. The range of L. microdon appears to extend in a northeast to southwest trajectory from Ranomafana National Park to Andringitra National Park. The southern limit of L. betsileo most likely is the Namorona River.

Etymology. — The name *betsileo* is proposed for this species and is derived from the Malagasy tribe from the Fianarantsoa region.

Vernacular Names.—Betsileo Sportive Lemur.

Lepilemur fleuretae, New Species

Type Series.—Whole blood for AND20 (TK125559/TTU104492), adult male, is stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the TTU catalog number. AND20 was collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Edward Louis on 12 May 2004.

Type Locality.—MADAGASCAR, Province de Toliary, Manangotry, Andohahela National Park (approximately 24°45'46.0"S, 046°51'47.0"E).

Description.—This sportive lemur is mediumsized (0.80 kg) with predominantly gray pelage, with a grayish-brown mixture along the proximal portion of the extremities. The pelage is noticeably lighter over the eyelids from the rest of the face. Running along the midline, a diffus stripe is present, starting from the forehead and continuing approximately halfway down the back. The venter is a lighter brownish gray with some light brown along the lateral edges of the belly. The tail is reddish gray proximally, becoming darker gray towards the tip.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, L. fleuretae differs from its closest relative by genetic distance, L. mustelinus, by $7.7\%\pm1.0\%$ (59 informative sites), $1.5\%\pm0.4\%$ (19 informative sites), and 4.5%±0.4% (177 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, L. fleuretae differs from its closest relatives by both geographic and genetic distance from two other new species, L. jamesi and L. wrighti, by $7.6\%\pm1.1\%$ (44 informative sites) and $10.2\%\pm1.2\%$ (70 informative sites), 1.9%±0.5% (18 informative sites) and $3.1\% \pm 0.5\%$ (27 informative sites), and $4.3\% \pm 0.7\%$ (113 informative sites) and 7.6%±0.6% (187 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, L. fleuretae differs from its closest relative by geographic distance, L. leucopus, by 14.1%±1.5% (92 informative sites), 7.0%±0.9% (62 informative sites), and 16.9%±0.8% (409 informative sites), respectively.

Distribution.—L. fleuretae is currently known from the Manangotry region, the rainforest parcel of Andohahela National Park between the Mandrare River to the west and the Mananara River to the north (Figure 8). The southern and northern distribution of L. fleuretae is confined to the rain forest within the boundaries of the Mandrare and Mananara Rivers. Further work needs to be conducted to confirm the extent of its range.

Comparisons and Remarks.—L. fleuretae is approximately the same size as L. jamesi, but is smaller than L. mustelinus and L. wrighti (Table 1). L. fleuretae is the most genetically divergent of all of the southeastern Lepilemur species with the exception of L. wrighti and L. microdon (Figures 2-8). The type series of L. microdon is located south of Fianarantsoa which sets the distribution of this recognized species at Ranomafana National Park (Andriaholinirina et al. 2006; Petter et al. 1977; Figure 8). Genetically, L. fleuretae is within the L. mustelinus clade representing the east coast Lepilemur group, whereas L. microdon is closely related to L. edwardsi, an east coast sportive lemur (Figures 2-7). Further studies should be conducted north of Manangotry to confirm the northern extent of L. fleuretae (Figure 8).

Etymology.—The name fleuretae is proposed in honor of Madame Fleurete Andriantsilavo, former Secrétarire Général du MINENVEF. Madame Fleurete worked tirelessly and constantly strove for the long term conservation of Madagascar's protected and unprotected areas.

Vernacular Names.—Fleurete's Sportive Lemur.

Lepilemur grewcocki, New Species

Type Series.—Whole blood for H1H21 (TK125519/TTU104452), adult male; H1H22 (TK125520/TTU104453), adult female; and H1H23 (TK125521/TTU104454), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. H1H21,

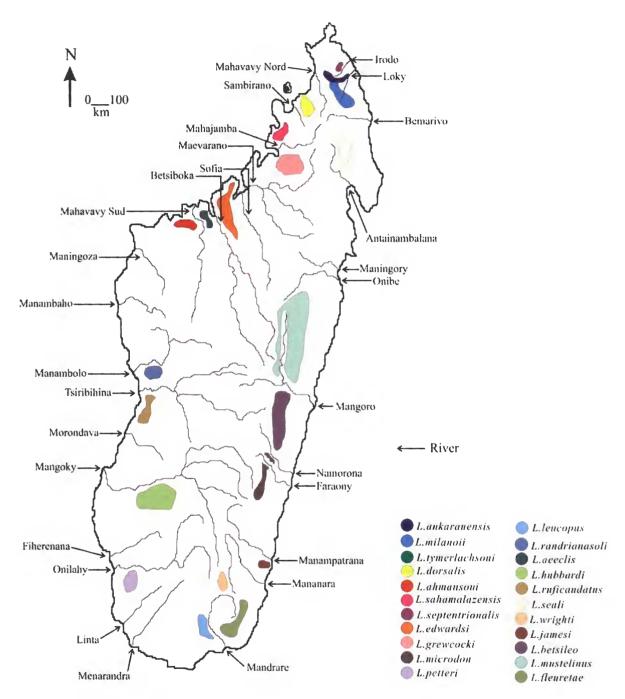


Figure 8. Proposed distribution of the sportive lemurs of Madagascar.

HIH21, HIH22, and HIH23 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantompohavana, and John R. Zaonarivelo on 13 November 2004.

Type Locality.—MADAGASCAR, Province de Mahajanga, Anjiamangirana Classified Forest (approximately 15°09'14.9"S, 047°43'41.0"E).

Description.—L. grewcocki is a medium-sized sportive lemur (0.78 kg) with a predominantly gray color pattern. The area around the mandible and the dorsal surface of the snout is whitish-pink in coloration. A dark stripe is present on the dorsal midline surface of the head. This black stripe may continue dorsally onto the back, but this character is individually variable. The venter is light gray to white. Unlike L. edwardsi, which has a consistently white tipped tail, the tail of L. grewcocki is entirely gray.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. grewcocki* differs from its closest relative by genetic distance, *L. edwardsi*, by 5.3%±1.0% (35 informative sites), 0.8%±0.3% (8 informative sites), and 2.8%±0.3% (66 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. grewcocki* differs from its closest relatives by geographic distance, *L. sahamalazensis*, by 6.8%±1.1% (51 informative sites), 4.8%±0.7% (40 informative sites), and 9.9%±0.6% (239 informative sites), respectively.

Distribution.—L. grewcocki currently is known from the Anjiamangirana region, south of the Mahajamba River and north of the Maevarano and Sofia Rivers.

Comparisons and Remarks.—L. grewcocki (0.78 kg) is smaller than L. edwardsi (1.10 kg), and larger than L. sahamalazensis (0.70 kg). Although L. grewcocki is located closer geographically to L. sahamalazensis, L. grewcocki is taxonomically more closely related to the western sportive lemur, L. edwardsi, and southeastern sportive lemur, L. microdon (Figures 2-6). Further studies should be conducted north of Ankarafantsika National Park to determine the northern extent of L. edwardsi, and south of Anjiamangirana to determine the southern extent of L. grewcocki (Figure 8).

Etymology.—The name grewcocki is proposed in honor of Bill and Berniece Grewcock who have generously supported our fieldwork in Madagascar and provided the laboratories and housing for all of the Malagasy graduate students in Omaha. The Grewcock's support is instrumental, transferring conservation related technology to the future Malagasy scientists.

Vernacular Names.—Grewcock's Sportive Lemur.

Lepilemur hubbardi, New Species

Type Series.—Whole blood for ZOMB9 (TK125558/TTU104491), adult female; ZOMB12 (TK125556/TTU104489), adult male; and ZOMB15 (TK125557/TTU104490), adult male; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. ZOMB9, ZOMB12, and ZOMB15 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Rambinintsoa Andriantompohavana on 15 March 2004, 15 March 2003, and 16 March 2003, respectively.

Type Locality.—MADAGASCAR, Province de Toliary, Zombitse National Park (approximately 22°53'18.7"S, 044°41'43.3"E).

Description.—L. hubbardi is a large-sized sportive lemur (0.99 kg) with reddish-brown, gray, and white pelage. The face is grayish-brown around the muzzle and eyes with a reddish-brown dorsal surface crown. The fur around the neck is lighter, forming a reddish blonde collar. The dorsum is dark reddish-brown around the shoulders and upper back, gradually becoming a lighter reddish-white to gray towards the base of the tail and hips. The venter is entirely white. The tail is uniformly reddish blonde.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. hubbardi* differs from its closest relative by geographic and genetic distance, *L. ruficaudatus*, by 6.4%±1% (41 informative sites), 1.4%±0.4% (15 informative sites), and 3.5%±0.3% (141 informative sites), respectively.

Distribution.—L. hubbardi is currently only known from the Zombitse National Park region, north of the Onilahy River and south of the Mangoky River.

Comparisons and Remarks.—L. hubbardi (0.99 kg) is larger in size than L. ruficaudatus (0.86 kg). Two phenotypes have been seen in Zombitse National Park. Currently, the sample size is too small to categorically determine if the phenotypes are sexually dichromatic. Additional survey work is required to determine the southern range of L. hubbardi and the northern extent of L. ruficaudatus (Figure 8).

Etymology.—The name hubbardi is proposed in honor of Theodore F. and Claire M. Hubbard Family Foundation for their generous support of Malagasy graduate students in the field and in the laboratory at Henry Doorly Zoo's Center for Conservation and Research (CCR). By providing the new laboratory and housing for the CCR's Genetics Department, the Hubbard Family Foundation's support will continue to be instrumental in transferring conservation related technology to the future Malagasy scientists.

Vernacular Names.—Hubbard's Sportive Lemur.

Lepilemur jamesi, New Species

Type Series.—Whole blood for M140 (TK125538/TTU104471), adult male; M141 (TK125539/TTU104472), adult male; and M142 (TK125540/TTU104473), adult male; are stored and curated at Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. M140, M141, and M142 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, John R. Zaonarivelo, and Edward Louis on 13 November 2000.

Type Locality.—MADAGASCAR, Province de Fianarantsoa, Manombo Special Reserve (approximately 23°01'69.5"S, 047°43'84.1"E).

Description.—L. jamesi is a large sized sportive lemur with primarily brown pelage. The face is demarcated into a mask, with whitish gray marking

along the jaw and throat from the chin to the ears. The dorsum of the head is brown with a black midline which is continuous for almost the entire length of the body. The dorsal region of the large cupped shaped ears is gray with the borders edged with black. There is usually a small cream colored patch restricted to the region beneath the ears. The venter is primarily brown, but a lighter shade than the dorsal pelage. Grayish-brown pelage is found around the ventral surface of the extremities and belly. The tail is brown proximally, gradually becoming a darker brown to black distally. The pelage is shorter than *L. fleuretae* and *L. betsileo*, giving the smooth appearance to the coat.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. jamesi* differs from its closest relatives (two newly described species) by geographic and genetic distance, *L. betsileo* and *L. fleuretae*, by 5.8%±1% (34 informative sites) and 7.6%±1.1% (44 informative sites), 1%±0.3% (8 informative sites), and 1.8%±0.2% (41 informative sites) and 4.3%±0.7% (113 informative sites), respectively.

Distribution.—*L. jamesi* is currently known from Manombo Special Reserve region, south of the Manampatrana River and north of the Mananara River.

Comparisons and Remarks.—L. jamesi (0.78 kg) is approximately the same size as L. fleuretae (0.80 kg), but L. jamesi is smaller than L. betsileo (1.11 kg). Additional survey work is required to determine the precise southern and northern range of L. jamesi (Figure 8). These two rivers already act as barriers for two other species, "pure" Eulemur albocollaris and a proposed species of Microcebus (Louis et al. 2006; Mittermeier et al. 2006). L. jamesi is found in one of the few remaining low altitude, coastal, rain forests.

Etymology.—The name jamesi is proposed in honor of the Larry, Jeannette, and Barry James' Family for their generous and long term support of Malagasy graduate students in the field and in the laboratory at Henry Doorly Zoo's Center for Conservation and Research.

Vernacular Names. — James' Sportive Lemur.

Lepilemur milanoii, New Species

Type Series. - Whole blood for DAR4.7 (TK125516/TTU104449), adult female; DAR4.17 (TK125517/TTU104450), adult male; and DAR4.18 (TK125564/TTU104497), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. DAR4.7, DAR4.17, and DAR4.18 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Edward Louison 25 November 2004, 26 November 2004, and 26 November 2004, respectively. DAR5.1, adult male; and DAR5.2, female, are live vouchers maintained at Parc Botanique et Zoologique de Tsimbazaza; 2 x 2.0 mm biopsies from ear pinna and 1.0 cc of whole blood; tissues stored at Henry Doorly Zoo's Center for Conservation and Research. A Microchip pit tag was placed subcutaneously between scapulae of DAR5.1 and DAR5.2 and recorded as 462C010E43 and 46506B0114, respectively. DAR5.1 and DAR5.2 were collected by Richard Randriamampionona, Gerard Nalanirina, and John R. Zaonarivelo on 18 October 2005. Complete measurements are available in Appendix Ia.

Type Locality.—MADAGASCAR, Province de Antsiranana, Daraina, Andranotsimaty (approximately 13°08'52.5"S, 049°41'11"E).

Description.—L. milanoii is reddish-brown on back and grayish-white on the venter. The head is reddish-brown dorsally, but gray brown on the face, forming a mask appearance. A diffuse darker brown midline stripe in found on the dorsum of the head, continuing partially down the back. The anterior portion of the thighs is reddish-brown, but the majority of the limbs are gray in color. The pelage is long and thick, and missing portions of the pelage, especially on the posterior limbs prominently gray, contrasting from the reddish-brown surrounding fur. The tail is uniformly reddish-brown.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. milanoii* differs from its closest relatives by geographic and genetic distance, *L. ankaranensis*, *L. septentrionalis*, and *L. dorsalis*,

by $2.7\%\pm0.6\%$ (20 informative sites), $5.9\%\pm1\%$ (38 informative sites), and $5.1\%\pm0.9\%$ (39 informative sites); $1.9\%\pm0.4\%$ (18 informative sites), $4.4\%\pm0.6\%$ (38 informative sites), and $2.9\%\pm0.5\%$ (25 informative sites); and $1.2\%\pm0.2\%$ (33 informative sites). $8.4\%\pm0.5\%$ (198 informative sites), and $4.2\%\pm0.3\%$ (100 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, L. milanoii differs from another species that is geographically close and newly described, L. tymerlachsoni, by a genetic distance of $2.5\%\pm0.6\%$ (18 informative sites), $2.1\%\pm0.5\%$ (18 informative sites), and $2.3\%\pm0.3\%$ (54 informative sites), respectively.

Distribution.—L. milanoii is currently known from the Daraina region, south of the Loky River. L. milanoii has been identified with molecular data in Andrafiamena Classified Forest. L. ankaranensis has also been identified at Andrafiamena Classified Forest.

Comparisons and Remarks.—L. milanoii (0.72 kg) is approximately the same size as L. dorsalis (0.73) kg), smaller than L. ankaranensis (0.79 kg), but larger than L. septentrionalis (0.6 kg). Although L. milanoii has been identified within the range of L. ankaranensis at Andrafiamena Classified Forest, L. milanoii is the only species found at Daraina. Additionally, L. milanoii has not been found at Ankarana or Analamera National Parks which has only L. ankaranensis. The Loky River is currently the northern barrier for *Propithecus tatter*salli, but L. milanoii has managed to cross this barrier, probably towards the river's source when there was an intact forest track between Daraina and Andrafiamena (Figure 8). Further studies should be conducted south of Andrafiamena Classified Forest and the southwestern limit of the Loky River to determine the distribution of L. milanoii. Additionally, extensive population studies should be conducted at Andrafiamena Classified Forest to determine the population dynamics of the two species found there.

Etymology.—The name milanoii is proposed for the Daraina region and is derived from the Malagasy language and means, "to swim". The Malagasy people refer to the Daraina region as "Daraina milanoa" which means "Daraina swimming" in reference to their swimming in the Andranotsimaty River looking for gold. Vernacular Names.—Daraina or Swimming Sportive Lemur.

Lepilemur petteri, New Species

Type Series.-Whole blood for BEZ15 (TK125511/ TTU104444), adult female; BEZ18 (TK125563/ TTU104496), adult male; and BEZ21 (TK125512/ TTU104445), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. BEZ15, BEZ18, and BEZ-21 were collected by Richard Randriamampionona and Edward Louis on 5 March 2001, 5 March 2001, and 6 March 2001, respectively. According to Jenkins (1987), a specimen, ZD.1892.111.61, (skull) is held at the British Museum of Natural History from the Ambolisatra Forest (23°03'S, 043°24"E) which is located within the tentative range of L. petteri.

Type Locality.—MADAGASCAR, Province de Toliary, Beza-Mahafaly (approximately 23°39'11.4"S, 044°37'90.6"E).

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. petteri* differs from its closest relative by geographic and genetic distance, *L. leucopus*, by 3.4%±0.8% (21 informative sites), 1.1%±0.3% (9 informative sites), and 1.8%±0.2% (46 informative sites), respectively.

Distribution.—*L. petteri* is currently known from the Beza-Mahafaly region, south of the Onilahy River and west of the Linta and Menarandra Rivers.

Description.—L. petteri is larger than L. leucopus with a similar gray to grayish-brown body (Table 1). The venter is whitish-gray. The face is gray with lighter circular patches around the eyes and under the chin. The ears are trimmed in lighter fur with the anterior or inner lining of the ear dark brownish-gray which highlights the ear. There is diffuse brownish-gray pelage on the anterior aspect of the thigh and along the dorsal midline.

Comparisons and Remarks.—L. petteri (0.63 kg) is larger than L. leucopus (0.54 kg). L. petteri is

located in primarily deciduous thicket or thorn scrub (spiny) and in the limited gallery forests. *L. leucopus* is found in the spiny desert forest parcels of Andohahela National Park. Further studies should be conducted north of Onilahy River to determine the northern extent of *L. petteri*. Additionally, further studies should be conducted in the remaining forest regions around the Linta and Menarandra Rivers to determine the distribution of both *L. petteri* and *L. leucopus* (Figure 8).

Etymology.—The name petteri is proposed in honor of Jean-Jacques Petter for his immense body of work on lemurs, including the sportive lemurs. Considered a leader in French Primatology, Dr. Petter was a winner of the WWF Gold Medal in 1981 for his conservation work in Madagascar.

Vernacular Names.—Petter's Sportive Lemur.

Lepilemur seali, New Species

Type Series.—Whole blood for JAR2 (TK125523/TTU104456), adult male; JAR3 (TK125524/TTU104457), adult female; and JAR8 (TK125525/TTU104458), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. JAR2, JAR3, and JAR8 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Edward Louison 19 July 2001, 19 July 2001, and 21 July 2001, respectively.

Type Locality.—MADAGASCAR, Province de Antsiranana, Anjanaharibe-Sud Special Reserve (approximately 14°47'45.1"S, 049°27'88.5"E).

Description.—L. seali is a large-sized sportive lemur (0.95 kg) with a uniform light chocolate-brown to reddish-brown color pattern. The venter is lighter brownish-gray and the pelage is extremely long and thick throughout the body. The face is light brownish-gray and is uniform in color. The hands and feet are a lighter grayish-brown. The tail, in contrast to the rest of the body, is brownish-gray throughout its length.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. seali* differs from its closest relative by genetic distance, *L. mustelinus*, by 10.1%±1.1% (70 informative sites), 4.4%±0.6% (43 informative sites), and 10.7%±0.6% (274 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. seali* differs from its closest relatives by geographic distance, *L. wrighti*, a newly described species found at Kalambatritra Special Reserve, by 9.2%±1.1% (79 informative sites), 4.3%±0.6% (37 informative sites), and 10.1%±0.5% (242 informative sites), respectively.

Distribution.—*L. seali* is currently known from the Anjanaharibe-Sud region, north of the Antainambalana River.

Comparisons and Remarks.—L. seali (0.95 kg) is approximately the same size as L. mustelinus (0.99 kg) and L. wrighti (0.95 kg). Although L. seali is located closer geographically to L. mustelinus, L, seali is taxonomically closer related to the southeastern sportive lemur, L. wrighti (Figures 2-8). Additional survey work is required to determine the southern range of L. seali and the northern extent of L. mustelinus. Currently, we have assigned the sportive lemur from Mananara-Nord (south of the Antainambalana River) to L. seali even though the available molecular data suggests that this population will be described as a separate species in the future, pending further field studies. Further studies also should be conducted north of Anjanaharibe-Sud Special Reserve to determine the northern extent of *L*. seali (Figure 8).

Etymology. —The name seali is proposed in honor of Dr. Ulysses Seal, an architect of the Conservation Breeding Specialist Group SSC/IUCN, and a definitive leader, teacher, and motivator of in situ conservation throughout the world.

Vernacular Names.—Seal's Sportive Lemur.

Lepilemur tymerlachsoni, New Species

Type Series.—Whole blood for LOKO4.2 (TK125535/TTU104468), adult male; LOKO4.5 (TK125537/TTU104470), adult female; and LOKO4.33

(TK125536/TTU104469), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. LOKO4.2, LOKO4.5, and LOKO4.33 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantompohavana, and John R. Zaonarivelo on 6 July 2004, 6 July 2003, and 9 July 2004, respectively.

Type Locality.—MADAGASCAR, Province de Antsiranana, Nosy Be, Lokobe National Park (approximately 13°23'27.6"S, 048°18'15.2"E).

Description.—L. tymerlachsoni is light brownish-gray with the upper half of the back a lighter reddish-brown. The venter is a light grayish-white. The anterior aspects of the thighs and edges of the extremities also have a light reddish-brown diffuse color. A dark brown to black midline dorsal stripe is present from the head to the lower half of the back. The face is gray with the appearance of a mask. The tail is an uniform light reddish-gray to brown.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. tymerlachsoni* differs from its closest relatives by both genetic and geographic distance, *L. milanoii*, *L. ankaranensis*, *L. dorsalis*, and *L. sahamalazensis*, by $2.5\%\pm0.6\%$ (18 informative sites), $3.9\%\pm0.8\%$ (25 informative sites), $4.9\%\pm1\%$ (33 informative sites), and $4.4\%\pm0.9\%$ (30 informative sites); $2.1\%\pm0.5\%$ (18 informative sites), $2.2\%\pm0.5\%$ (20 informative sites), $2.2\%\pm0.5\%$ (20 informative sites); $2.3\%\pm0.3\%$ (54 informative sites), $2.3\%\pm0.3\%$ (55 informative sites), $4.7\%\pm0.4\%$ (110 informative sites), and $4.8\%\pm0.4\%$ (126 informative sites), respectively.

Distribution.—L. tymerlachsoni is currently known from the Lokobe region and Nosy Be Island.

Comparisons and Remarks.—L. tymerlachsoni (0.88 kg) is larger than L. milanoii (0.72 kg), L. sahamalazensis (0.70 kg), L. dorsalis (0.73 kg), L. ankaranensis, and L. septentrionalis (0.60 kg). Andriaholinirina et al. (2006) presented data that distinguished *L. sahamalazensis* from *L. dorsalis* (Ambanja/Nosy Be), but the morphological and molecular data clearly separate *L. dorsalis* (Manongarivo/Antafondro) and *L. tymerlachsoni* (Nosy Be), and is comparable to differences between the other northern recognized sportive lemurs (Figures 2-8).

Etymology,—The name tymerlachsoni is proposed in honor of the Howard and Rhonda Hawk Family who have made generous contributions to the Madagascar Project, providing infra-structure and field support to the many Malagasy graduate students.

Vernacular Names.—Hawk's Sportive Lemur.

Lepilemur wrighti, New Species

Type Series.—Whole blood for KALA4.9 (TK125527/TTU104460), adult female; KALA4.16 (TK125565/TTU104498), adult male; and KALA4.18 (TK125526/TTU104459), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. KALA4.9, KALA4.16, and KALA4.18 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantompohavana, and Edward Louis on 12 June 2004, 12 June 2003, and 14 June 2004, respectively.

Type Locality.—MADAGASCAR, Province de Toliary, Kalambatritra Special Reserve, Befarara (approximately 23°25'05.4"S, 046°26'55.4"E).

Description.—L. wrighti is a large-sized lemur with a diffuse reddish-brown and gray pelage. The dorsum is reddish-brown to grayish-brown. The venter is grayish-brown, lighter in color than the dorsum. The head of females is uniformly gray, sharply contrasting with the rest of the body. The males have a diffuse reddish brown to gray appearance that does not contrast dramatically with the body. Thus, based on our limited sample size (n = 5), L. wrighti represents the first instance of sexual dichromatism in the genus Lepilemur. Furthermore, in some individual females, there is a slight color change around the face that forms

a mask-like appearance. For both sexes, the ears have minimal to short fur and are lighter in color.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. wrighti* differs from its closest relatives by genetic distance, *L. seali* and *L. fleuretae*, by 9.2%±1.1% (79 informative sites) and 10.2%±1.2% (70 informative sites); 4.3%±0.6% (37 informative sites) and 3.1%±0.5% (27 informative sites); and 10.1%±0.5% (242 informative sites) and 10.8%±0.5% (187 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. wrighti* differs from its closest relative geographically, *L. leucopus*, by genetic distance of 13.9%±1.4% (99 informative sites), 3.1%+0.5% (27 informative sites), and 16.4%±0.8% (395 informative sites), respectively.

Distribution.—L. wrighti is currently known from Kalambatritra Special Reserve, west of the Mananara River and north of the Mandrare River.

Comparisons and Remarks.—L. wrighti (0.95 kg) is a large sized sportive lemur, approximately the same size as L. mustelinus (0.99 kg), but larger than L. fleuretae (0.80 kg). With its close taxonomic relationship with the northeastern sportive lemur, L. seali, and its distinctive morphological appearance, the species is well differentiated from other sportive lemurs in eastern Madagascar. Further studies need to be conducted to determine its distribution (Figure 8) and to verify the possible pelage difference between males and females.

Etymology.—The name wrighti is proposed in honor of Dr. Patricia Wright for her long term dedication and contributions to conservation in Madagascar and tropical environments throughout the world.

Vernacular Names.—Wright's Sportive Lemur.

As with all of the lemur taxa of Madagascar, comprehensive census and taxonomic studies of free-ranging populations in the Genus *Lepilemur* are necessary for the implementation of management and conservation programs. The existing distribution records for all of the *Lepilemur* species are limited (Thalmann and Ganzhorn 2003). Furthermore, the molecular data from previous studies regarding multiple lemur species reflects specific biases to regions of

the mitochondrial DNA; and therefore, data sets based on independent vouchers or sample sets are difficult to correlate (Andriaholinirina et al. 2006; Pastorini et al. 2003; Wyner et al. 1999; Yoder et al. 2000). Although the sequence data presented in this paper are not all-inclusive nor equivalent to every lemur mtDNA study or region, the authors for the first time present sequence data from three regions of the mtDNA in an attempt to submit not only new data, but also to correlate the data with previous studies. By developing an equivalent data set with respect to the various regions of the mtDNA sequenced by the various researchers, a comprehensive and cumulative approach could be created that would link independent but complementary research programs.

The processes of evolution are an important component of species concepts, science, and investigation. The PSC not only encompasses a cladistic perspective, but also allows the biologist to focus operationally on the results of evolution to present and to delineate species. A cumulative approach implementing morphological, cytogenetic, and molecular data would be the ideal approach when defining species (Mayor et al. 2004; Mittermeier et al. 2006). The fine-tuning of dynamic population studies will require constant and consistent addition of nuclear and mitochondrial DNA data from multiple individuals from all geographic ranges to this data set. Results derived from such a data set would be instrumental in making accurate, precise, and responsible management decisions by wildlife and conservation entities.

By applying the phylogeographic studies by Pastorini et al. (2003) and Thalmann (2000), geographic barriers can be defined that affect multiple taxa, including both flora and fauna. By establishing and prioritizing these phylogeographic regions, conservation management decisions can be implemented that will support the preservation of biodiversity within these critically

defined regions. Superimposition of the new *Lepilemur* species' distributions on a geophysical map indicates that the rivers are forming significant barriers, contributing to the processes of speciation. Additionally, an inverse relationship appears to exist between body size and number of species with the smaller body sized genera containing the greater number of species. This effect appears to be more amplified in the nocturnal lemurs which have smaller territories than the larger bodied diurnal lemurs, with rivers forming the limiting boundaries for each species. The eastern Lepilemur species also appear to have less dense populations than the species found in northern and western Madagascar. Correlating Microcebus and Avahi sequence data to the distributions of the 22 Lepilemur species, a geophysical map is created which indicates a comparative partitioning based on unique species, with their distributions bounded by the same river systems or pairs (unpublished data; Louis et al. 2006). The known distributions of the mid-sized diurnal lemurs, for example, the Genus Eulemur, also corresponds to the Lepilemur species distributions. Even a cursory glance at the geophysical map and the distributions of the 22 sportive lemurs, allows researchers to predict areas where new species likely exist; therefore, more effectively concentrating research efforts (Figure 8).

The extreme degree of regional endemism, the continued risk from human encroachment, and the restricted geographic ranges combined with the inadequate knowledge of established distributions of described lemurs across Madagascar, emphasizes the need for further investigations in unexplored sites and the re-evaluation of protective measures, conservation ranking, and management of these species. The limited knowledge of geographic limits should be a major priority for conservationists and scientists alike.

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APPENDIX I

The following Appendices to this publication are available online at the indicated website addresses.

a. *Lepilemur* Field Data (Individual data file for each *Lepilemur*, including morphometrics, photos, sequence accessions, global position system, microchip data, gender, and location):

http://10.10.10.3/ccr/genetics/lemur/index.asp?page=ccr/genetics/lemur/Megaladapidae.htm

b. Map Figure 1 (Maps of historical distributions):

http://www.omahazoo.com/ccr/genetics/papers/appendix1.pdf

c. Primer Table 1 (Summary of designed primers for D-loop, 12s rRNA, and PAST fragments):

http://www.omahazoo.com/ccr/genetics/papers/appendixprimertablel.pdf

d. Pairwise Data Table II (Complete pairwise matrices):

http://www.omahazoo.com/ccr/genetics/papers/appendixtablell.pdf

e. Pairwise Aggregate Analysis Figure 2 (Complete PAA for Summary of the D-loop, 12s rRNA, and PAST fragments):

Figure 2A, D-loop PAA - http://10.10.10.3/ccr/genetics/papers/d-loop.pdf

Figure 2B, 12s rRNA PAA - http://10.10.10.3/ccr/genetics/papers/rRNA.pdf

Figure 2C, PAST PAA - http://10.10.10.3/ccr/genetics/papers/pastorini.pdf

f. Haplotype Summary List Figure 3 (Summary List of the *Lepilemur* Haplotypes for D-loop, 12s rRNA, and PAST fragments):

http://www.omahazoo.com/ccr/genetics/papers/appendixIII.pdf

g. Sequence Summary Table III (Summary of the D-loop, 12s rRNA, and PAST fragments):

http://www.omahazoo.com/ccr/genetics/papers/appendixtableIII.pdf

h. Bayesian D-loop Figure 4 (Bayesian analysis of the D-loop for 211 *Lepilemur*):

http://www.omahazoo.com/ccr/genetics/papers/appendixfigure4.pdf

i. Message Passing Cluster Figure 5 (Message Passing Cluster analysis of D-loop for 211 *Lepilemur*):

http://www.omahazoo.com/ccr/genetics/papers/appendixfigure5.pdf

APPENDIX II

Samples (211 Lepilemur and 19 outgroups total) used in the present genetic study and taxonomic revision of the Madagascar lemur genus Lepilemur. "TK Number is referenced voucher curated at The Museum of Texas Tech University. *Mitochondrial DNA sequence data for 12s rRNA (12s rRNA subunit gene), PAST (Pastorini Fragment), and D-loop (D-loop or control region) for each sample are available from GenBank under the listed accession numbers.

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST⁵	D loop ^b
ANAL5	TK125502	Analamera	Lepilemur ankarunensis	Lepilemur ankaranensis	AF474184	AY582564	AY769363
ANAL13	TK125501	(Antobiratsy) Analamera (Antobiratsy)	Lepilemur ankaranensis	Lepilemur ankaranensis	AF474185	AY582565	AY769364
ANAL2.1		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192608	AY582566	AY769365
ANAL2.2		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192609	AY582567	AY769366
ANAL2.4		Analamer (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192610	AY582568	AY769367
ANAL2.12		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192611	AY582569	AY769368
ANAL2.13		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192612	AY582570	AY769369
ANAL2.29		Analamera (Ankavanana)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192613	AY582571	AY769370
CAR6		Ankarana (Anilotra)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192614	AY582572	AY769371
CARII		Ankarana (Anilotra)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192615	AY 582573	AY769372
CAR15		Ankarana (Anilotra)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192616	AY582574	AY769373
CAR17		Ankarana (Anilotra)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192617	AY582575	AY769374
CAR21		Ankarana (Anilotra)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192618	AY582576	AY769375
CAR33		Ankarana (Andriafiabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192619	AY582577	AY769376
CAR43		Ankarana (Andriafiabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192620	AY582578	AY769377
CAR45		Ankarana (Andriafiabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192621	AY582579	AY769378

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST	D loop ^b
CAR46		Ankarana (Andriafiabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192622	AY582580	AY769379
CAR58		Ankarana (Anilotra)	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192623	AY582581	AY769380
CAR59		Ankarana	Lepilemur ankaranensis	Lepilemur ankaranensis	AY192624	AY582582	AY769381
MER24	TK125545	(Annoua) Analamera (Antobiratev)	Lepilemur ankaranensis	Lepilemur ankaranensis	AF474211	AY582583	AY 769382
MER26		Analamera Antohiratsy)	Lepilemur ankaranensis	Lepilemur ankaranensis	AF474212	AY582584	AY769383
LABE5.1		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529447	DQ529739	DQ529597
LABE5.2		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529448	DQ529740	DQ529598
LABE5.3		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529449	DQ529741	DQ529599
LABE5.4		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529450	DQ529742	DQ529600
LABE5.17		Analamera (Analabe)	Lepilemur ankaranensis	Lepilemur ankaranensıs	DQ529451	DQ529743	DQ529601
FIA5.1		Andrafiamena (Anjakely)	Lepilennir ankaranensis	Lepilemur ankaranensis	DQ529422	DQ529714	DQ529572
FIA5.5		Andrafiamena (Anjakely)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529423	DQ529715	DQ529573
FIA5.6		Andrafiamena (Anjakely)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529424	DQ529716	DQ529574
FIA5.7		Andrafiamena (Anjakely)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529425	DQ529717	DQ529575
FIA5.8		Andrafiamena (Anjakely)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529426	DQ529718	DQ529576
FIA5.9		Andrafiamena (Anjakely)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529427	DQ529719	DQ529577
F1A5.10		Andrafiamena	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529428	DQ529720	DQ529578
FIA5.11		(Anjakely) Andrafiamena	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529429	DQ529721	DQ529579
F1A5.12		(Anjakely) Andrafiamena (Anjakely)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529430	DQ529722	DQ529580

FIA5.13 LAME5.6 LAME5.8 FARY5.1 TK FARY5.2 FARY5.3 FARY5.4 LAVA5.1 LAVA5.1 LAVA5.1 LAVA5.3 LAVA5.3 TK			Designation	Designation	rRNAb		
		Andrafiamena (Anjakelv)	Lepilemur ankaranensis	Lepilemur ankaranensis	DQ529431	DQ529723	DQ529581
		Analamera (Ankavanana)	Lepilemur ankaranensis	Lepileunur ankaranensis	DQ529420	DQ529712	DQ529570
		Analamera (Ankavanana)	Lepilentur ankaranensis	Lepilemur ankaranensis	DQ529421	DQ529713	DQ529571
	TK125515	Sahafary	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529432	DQ529724	DQ529582
		(Sahafary) Sahafary (Sahafary)	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529433	DQ529725	DQ529583
		(Sahafary	Lepilemnr septentrionalis	Lepilemur septentrionalis	DQ529434	DQ529726	DQ529584
		Sahafary Sahafary	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529435	DQ529727	DQ529585
		(Sanatary) Sahafary	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529436	DQ529728	DQ529586
	TK125532	Sahafary	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529437	DQ529729	DQ529587
		Sahafary (Analalava)	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529438	DQ529730	DQ529588
	TK125566	Sahafary	Lepilemur septentrionalis	Lepilemur septentrionalis	DQ529439	DQ529731	DQ529589
KALA24		(Alialalava) Kalambatritra	Lepilemur microdon	Lepilemur wrighti	DQ529531	DQ529641	DQ529499
KALA4.9 TK	TK125527	Kalambatritra	Lepilemur microdon	Lepilemur wrighti	DQ529356	DQ529646	DQ529504
KALA4.16 TK	TK125565	(Betafata) Kalambatritra	Lepilemur microdon	Lepilemur wrighti	DQ529357	DQ529647	DQ529505
KALA4.18 TK	TK125526	(Betarara) Kalambatritra (Boforgas)	Lepilemur microdon	Lepilemur wrighti	DQ529358	DQ529648	DQ529506
KALA4.19		(Detalala) Kalambatritra (Boforora)	Lepilemur microdon	Lepilemur wrighti	DQ529359	DQ529649	DQ529507
KALA5.12		(Dotalara) Kalambatritra (Sahalaya)	Lepilemur microdon	Lepilemur wrighti	DQ529419	DQ529711	DQ529569
DAR4.7 TK	TK125516	Daraina (Andranotsimaty)	Lepilemur ankaranensis	Lepilemur milanoii	DQ529329	DQ529619	DQ529477
DAR4.17 TK	TK125517	Daraina (Andranotsimaty)	Lepilemur ankaranensis	Lepilemur milonoii	DQ529330	DQ529620	DQ529478

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST	D loop ^b
DAR4.18	TK125564	Daraina	Lepilemur ankaranensis	Lepilemur milanoii	DQ529331	DQ529621	DQ529479
DAR4.19		Daraina	Lepilemur ankaranensis	(Andranotsimaty) Lepilemur milanoii	DQ529332	DQ529622	DQ529480
DAR4 23		Daraina	Lepilemur ankaranensis	(Andranotsimaty) Lepilemur milanoii	DO529333	DQ529623	DQ529481
				(Andranotsimaty)	, (000000000000000000000000000000000000000
DAR4.27		Daraina	Lepilemur ankaranensis	Lepilemur milanoii (Andranotsimatu)	DQ529334	DQ529624	DQ529482
DAR4.28		Daraina	Lepilemur ankaranensis	(Antalanoismaty) Lepilemur milanoii	DQ529335	DQ529625	DQ529483
DAR4.30		(Andranotsımaty) Daraina	Lepilemur ankaranensis	Lepilemur milanoii	DQ529336	DQ529626	DQ529484
DAR4.35		(Andranotsimaty) Daraina	Lepilemur ankaranensis	Lepilemur milanoii	DQ529337	DQ529627	DQ529485
DAR4.41		(Andranotsimaty) Daraina	Lepilemur ankaranensis	Lepilemur milanoii	DQ529338	DQ529628	DQ529486
DAR5.1		(Andranotsimaty) Daraina	Lepilemur ankaranensis	Lepilemur milanoti			
DAR52		(Andranotsimaty)	I enilemur ankaranensis	ionalim milanoii			
Z: CXXX		(Andranotsimaty)					
GARI	TK125518	Manongarivo	Lepilemur dorsalis	Lepilemur dorsalis	AY192625	AY582592	AY769391
ANT5.2		Antafondro	Lepilemur dorsalis	Lepilemur dorsalis	DQ529440	DQ529732	DQ529590
ANT5.5		(Maromiandra) Antafondro	Lepilemur dorsalis	Lepilemur dorsalis	DQ529441	DQ529733	DQ529591
1		(Maromiandra)	7	I amilamente doucedie	DO520442	DO520734	DO520502
AN15.6		Antaronaro (Maromiandra)	ьернетиг аогзанs	Lepnemar dorsans	74467670	FC/676XQ	7(5(75))
ANT5.7	TK125507	Antafondro	Lepilemur dorsalis	Lepilemur dorsalis	DQ529443	DQ529735	DQ529593
ANT5.11	TK125562	(Maronnanula) Antafondro	Lepilemur dorsalis	Lepilemur dorsalis	DQ529444	DQ529736	DQ529594
LAZA5.1	TK125533	(Maromiandra) Sahamalaza	Lepilemur dorsalis	Lepilemur sahamalazensis	DQ529445	DQ529737	DQ529595
LAZA5.10	TK125534	(Ankarata) Sahamalaza	Lepilemur dorsalis	Lepilemur sahamalazensis	DQ529446	DQ529738	DQ529596
LOK04.2	TK125535	(Ankaraia) Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529360	DQ529650	DQ529508

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST	D loop ^b
LOK04.5	TK125537	Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529361	DQ529651	DQ529509
LOK04.19		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529362	DQ529652	DQ529510
LOKO4.20		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529363	DQ529653	DQ529511
LOK04.23		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529364	DQ529654	DQ529512
LOK04.32		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529365	DQ529655	DQ529513
LOK04.33	TK125536	Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529366	DQ529656	DQ529514
LOK04.34		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529367	DQ529657	DQ529515
LOK04.35		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529368	DQ529658	DQ529516
LOK04.36		Lokobe	Lepilemur dorsalis	Lepilemur tymerlachsoni	DQ529369	DQ529659	DQ529517
ANK4		Ankarafantsika	Lepilemur edwardsi	Lepilemur edwardsi	AF474186	AY582585	AY769384
ANK16		Ankarafantsika	Lepilemur edwardsi	Lepilemur edwardsi	AF474187	AY582586	AY769385
KIBO22	TK125529	Tsiombikibo	Lepilemur aeeclis	Lepilemur ahmansoni	DQ529312	DQ529602	DQ529460
KIBO58	TK125530	Tsiombikibo	Lepilemur edwardsi	Lepilemur ahmansoni	DQ529313	DQ529603	DQ529461
KIBO65	TK125531	Tsiombikibo	Lepilemur edwardsi	Lepilemur ahmansoni	DQ529314	DQ529604	DQ529462
KIBO68		Tsiombikibo	Lepilemur aeeclis	Lepilemur ahmansoni	DQ529315	DQ529605	DQ529463
MARI		Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529316	DQ529606	DQ529464
MAR2		Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529317	DQ529607	DQ529465
MAR18	TK125541	Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529318	DQ529608	DQ529466
MAR20	TK125542	Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529319	DQ529609	DQ529467

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST	D loop ^b
MAR21		Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529320	DQ529610	DQ529468
MAR22	TK125543	Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529321	DQ529611	DQ529469
MAR23		Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529322	DQ529612	DQ529470
MAR27		Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529323	DQ529613	DQ529471
MAR36	TK125544	Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529324	DQ529614	DQ529472
MAR38		Mariarano	Lepilemur edwardsi	Lepilemur edwardsi	DQ529325	DQ529615	DQ529473
HIH21	TK125519	Anjiamangirana	Lepilemur edwardsi	Lepilemw grewcocki	DQ529326	DQ529616	DQ529474
HIH22	TK125520	Anjiamangirana	Lepilemur edwardsi	Lepilemur grewcocki	DQ529327	DQ529617	DQ529475
HIH23	TK125521	Anjiamangirana	Lepilemur edwardsi	Lepilemur grewcocki	DQ529328	DQ529618	DQ529476
AND65		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529339	DQ529629	DQ529487
AND66	TK125503	(Ivrangatsiaka) Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529340	DQ529630	DQ529488
AND67	TK125560	(Nangatsiaka) Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529341	DQ529631	DQ529489
AND68	TK125561	(Mangatsiaka) Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529342	DQ529632	DQ529490
AND69		(Mangatsiaka) Andohahela (Mangatsiaka)	Lepilemur leucopus	Lepilemur leucopus	DQ529343	DQ529633	DQ529491
AND78		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529344	DQ529634	DQ529492
AND79		(Mangatsiaka) Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529345	DQ529635	DQ529493
AND92		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529346	DQ529636	DQ529494
AND93		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529347	DQ529637	DQ529495
AND94		(Mangaisiaka) Andohahela (Mangatsiaka)	Lepilemur leucopus	Lepilemur leucopus	DQ529348	DQ529638	DQ529496

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNAb	PAST	D loop ^b
AZ05.6		Andohahela (Ihazofotsv)	Lepilemur leucopus	Lepilemur leucopus	DQ529409	DQ529701	DQ529559
HAZO5.7		Andohahela (Thazofotsv)	Lepilemur leucopus	Lepilemur leucopus	DQ529410	DQ529702	DQ529560
HAZO5.16		Andohahela (Thazofotsv)	Lepilemur leucopus	Lepilemur leucopus	DQ529411	DQ529703	DQ529561
HAZ05.17		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529412	DQ529704	DQ529562
HAZ05.18		Andohahela (Thazofotsy)	Lepilemur leucopus	Lepilemur leucopus	DQ529413	DQ529705	DQ529563
HAZ05.19		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529414	DQ529706	DQ529564
HAZO5.20		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529415	DQ529707	DQ529565
HAZ05.21		Andohahela (Thazofotev)	Lepilemur leucopus	Lepilemur leucopus	DQ529416	DQ529708	DQ529566
HAZ05.22		Andohahela	Lepilemur leucopus	Lepilemur leucopus	DQ529417	DQ529709	DQ529567
HAZ05.23		(mazolotsy) Andohahela (Thazofatey)	Lepilemur lencopus	Lepilemur leucopus	DQ529418	DQ529710	DQ529568
BEZ14		Beza-Mahafaly	Lepilemur lencopus	Lepilemur petteri	AF474191	AY582587	AY769386
BEZ15	TK125511	Beza-Mahafaly	Lepilemur leucopus	Lepilemur petteri	AF474192	AY582588	AY769387
BEZ18	TK125563	Beza-Mahafaly	Lepilemur leucopus	Lepilemur petteri	AF474193	AY582589	AY769388
BEZ21	TK125512	Beza-Mahafaly	Lepilemur leucopus	Lepilemur petteri	AF474194	AY582590	AY769389
BEZ22		Beza-Mahafaly	Lepilemur leucopus	Lepilemur petteri	AF474195	AY582591	AY769390
KELI	TK125528	Ranomafana (Vohinarara)	Lepilemur microdon	Lepilemur microdon	DQ529390	DQ529682	DQ529540
RANO234	TK125552	Ranomafana (Vohinarara)	Lepilemur microdon	Lepilemur microdon	AF474218	AY582596	AY769395
RAN0235		Ranomafana (Vohiparara)	Lepilemur microdon	Lepilemur microdon	AF474219	AY 582597	AY769396
RANO236		Ranomafana (Vohiparara)	Lepilemur microdon	Lepilemur microdon	AF474220	AY582598	AY769397

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RAN02.24		Ranomafana	Lepilemur microdon	Lepilemur microdon	AY585736	DQ529678	DQ529536
RAN02.25		Ranomafana	Lepilemur microdon	Lepilemur microdon	AY585737	DQ529679	DQ529537
RIR02		Ranomafana	Lepilemur microdon	Lepilemur microdon	DQ529407	DQ529699	DQ529557
RAN3.1		Ranomafana	Lepilemur microdon	Lepilemur microdon	DQ529408	DQ529700	DQ529558
PBZT111		Ranomafana	Lepilemur microdon	Lepilemur microdon	AY254494	AY582600	AY769399
TOL2.17	TK125555	(voniparara) Tolongoina	Lepilemur microdon	Lepilemur microdon	AF474224	AY582599	AY769398
VOP2.6		Ranomafana	Lepilemur microdon	Lepilemur microdon	DQ529388	DQ529680	DQ529538
VOP2.16		(Voniparara) Ranomafana	Lepilemur microdon	Lepilemur microdon	DQ529389	DQ529681	DQ529539
MIT16		(Voniparara) Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	AF474213	AY582604	AY769403
MIT17	TK125546	Anjahamena	Lepilemur ruficaudatus	Lepilemur aeeclis	AF474214	AY582605	AY769404
PBZT112	TK125551	Anjahamena	Lepilemur edwardsi	Lepilemur aeeclis	AY254493	AY582606	AY769405
PBZT119		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529380	DQ529670	DQ529528
JAM4.8		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529381	DQ529671	DQ529529
JAM4.9		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529382	DQ529672	DQ529530
JAM4.10	TK125522	Anjahamena	Lepilemur edwardsi	Lepilemur aeeclis	DQ529383	DQ529673	DQ529531
JAM4.11		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529384	DQ529674	DQ529532
JAM4.12		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529385	DQ529675	DQ529533
JAM4.13		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529386	DQ529676	DQ529534
JAM4.27		Anjahamena	Lepilemur aeeclis	Lepilemur aeeclis	DQ529387	DQ529677	DQ529535

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AND20	TK125559	Andohahela	Lepilemur microdon	Lepilemur fleuretae	DQ529401	DQ529693	DQ529551
ANJZ32	TK125504	Anjozorobe	Lepilemur mustelimus	Lepilemur mustelimus	DQ529349	DQ529639	DQ529497
ANJZ33	TK125505	Anjozorobe	Lepilemur mustelinus	Lepilemur mustelinus	DQ529350	DQ529640	DQ529498
ANOSIB15		(Annosibe an'ala	Lepilemur mustelinus	Lepilemur mustelimus	AF474188	AY582607	AY769406
ANOSIB18	TK125506	Anosibe an'ala	Lepilemur mustelinus	Lepilemur mustelinns	AF474189	AY582608	AY769407
BET21		Betampona	Lepitemm mustelimus	Lepilemur mustelirus	AF474190	AY582609	AY769408
FAN10		Fandriana	Lepitemur mustelimus	Lepilemur betsileo	AF474196	AY582610	AY769409
FAN11	TK125513	Fandriana	Lepilemur microdon	Lepilemur hetsileo	AF474197	AY582611	AY769410
FAN4.24	TK125514	Fandriana	Lepilemur microdon	Lepilemur betsileo	DQ529400	DQ529692	DQ529550
JOZO4.11		Anjozorobe	Lepilemur mustelinus	Lepilemur mustelimus	DQ529355	DQ529645	DQ529503
L5		Manombo	Lepilemur microdon	Lepitemur jamesi	AF474201	AY582620	AY769420
M83B		Manombo	Lepilemur microdon	Lepilemur jamesi	AF474202	AY582612	AY769411
M93B		Manombo	Lepilemur microdon	Lepilemur jamesi	AF474203	AY582613	AY769412
M94B		Manombo	Lepilemur microdon	Lepilemur jamesi	AF474204	AY582614	AY769413
M95B		Manombo	Lepilemur microdon	Lepilemur jamesi	AF474205	AY582615	AY769414
M104B		Manombo	Lepilemur microdon	Lepilemur jamesi	AF474206	AY582616	AY769415
M105B		Manombo	Lepilemur microdon	Lepilemur jamesi	AF474207	AY584480	AY769416
M140	TK125538	Manombo	Lepilemm: microdon	Lepilemur jamesi	AF474208	AY582617	AY769417
M141	TK125539	Manombo	Lepilemur microdon	Lepilemur jamesi	AF474209	AY582618	AY769418

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^h	PAST	D loop ^b
M142	TK125540	Manombo	Lepilemur microdon	Lepilemur jamesi	AF474210	AY582619	AY769419
MIZA3	TK125547	Maromizaha	Lepilemur mustelinus	Lepilemur mustelinus	DQ529403	DQ529695	DQ529553
MIZA11		Maromizaha	Lepilemur mustelinus	Lepilenur mustelinus	DQ529404	DQ529696	DQ529554
MIZA15		Maromizaha	Lepilenur mustelinus	Lepilemur mustelinus	DQ529405	DQ529697	DQ529555
MIZA18		Maromizaha	Lepilemur mustelimıs	Lepilemur mustelinus	DQ529406	DQ529698	DQ529556
SIN26		Tsinjoarivo	Lepilenur mustelinus	Lepilemur mustelinus	AF474221	AY582621	AY769421
SIN27		Tsinjoarivo	Lepilemur mustelimus	Lepilemur mustelinus	AF474222	AY582622	AY769422
TAD25		Mantadia	Lepilemur mustelinus	Lepilemur mustelinus	AF474223	AY582623	AY769423
TAD4.4	TK125554	Mantadia	Lepilemur mustelinus	Lepilemur mustelinus	DQ529391	DQ529683	DQ529541
TAD4.16	TK125553	Mantadia	Lepilemur mustelinus	Lepilemur mustelinus	DQ529392	DQ529684	DQ529542
TAD4.17		Mantadia	Lepilemur mustelimus	Lepilemur mustelinus	DQ529393	DQ529685	DQ529543
TAD4.19		Mantadia	Lepilemur mustelimus	Lepilemur mustelimis	DQ529394	DQ529686	DQ529544
TAD4.23		Mantadia	Lepilemur mustelimus	Lepilemur mustelinus	DQ529395	DQ529687	DQ529545
TAD4.58		Mantadia	Lepilemur mustelimus	Lepilemur mustelimus	DQ529396	DQ529688	DQ529546
TAD4.59		Mantadia	Lepilemur mustelinus	Lepilemur mustelinus	DQ529397	DQ529689	DQ529547
TAD4.60		Mantadia	Lepilemur mustelinus	Lepilemur mustelinus	DQ529398	DQ529690	DQ529548
TAD4.61		Mantadia	Lepilemur mustelinus	Lepilennur mustelinus	DQ529399	DQ529691	DQ529549
TSINJ36		Tsinjoarivo	Lepilemur mustelinus	Lepilemur nusstelinus	AF474225	AY582624	AY769424
TSIN137		Tsinjoarivo	Lepilemur mustelinus	Lepilemur mustelinus	AF474226	AY582625	AY769425
ZAH21		Zahamena	Lepilemur mustelinus	Lepilenur mustelinus	AF474227	AY582626	AY769426

Zahamena Lepilemur mustelimus Lepilemur mustelimus AF474228 AV582627 Zahamena Lepilemur mustelimus Lepilemur mustelimus AF474220 AV582630 Zahamena Lepilemur mustelimus Lepilemur mustelimus AF474230 AV582630 Zahamena Lepilemur mustelimus Lepilemur mustelimus AF474231 AV582630 TK125549 Beroboka Lepilemur rujkcandenus Lepilemur rujkcandenus AF474215 AV582601 TK12550 Beroboka Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus TK125509 TSingy de Bernaraha Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus TK125509 TSingy de Bernaraha Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus TK125556 Zombise Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur rujkcandenus TK125556 Zombise Lepilemur rujkcandenus Lepilemur rujkcandenus Lepilemur ruj	Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PASTb	D loop
25 Zabamena Lepilemur mustelinus Lepilemur mustelinus Lepilemur mustelinus AF474230 AYS82639 216 Zahamena Lepilemur mustelinus Lepilemur mustelinus AF474231 AYS82639 217 Zahamena Lepilemur mustelinus Lepilemur mustelinus AF474212 AYS82631 217 TK125548 Beroboka Lepilemur ruficandanus Lepilemur ruficandanus Lepilemur ruficandanus AF474212 AYS82601 147 TK125549 Beroboka Lepilemur ruficandanus	ZAH22		Zahamena	Lepilemur mustelinus	Lepilemur mustelimus	AF474228	AY582627	AY769427
201 Zahamena Lepilemur mustelinus Lepilemur mustelinus AF474231 AY582630 215 Zahamena Lepilemur mustelinus Lepilemur mustelinus AF474231 AY582630 217 Zahamena Lepilemur mustelinus Lepilemur mustelinus AF474212 AY582631 217 TK125548 Beroboka Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus AF474215 AY582601 142 TK125549 Beroboka Lepilemur ruficaudatus Lepilemur ruficaudatus AF474217 AY582603 AY582603 A5 TK125508 TSingy de Bernaraha Lepilemur ruficaudatus Lepi	ZAH25		Zahamena	Lepilemur mustelimus	Lepilemur mustelinus	AF474229	AY582628	AY769428
216 Zahamena Lepilennur mustelinus Lepilennur mustelinus AF474231 AV582630 217 Zahamena Lepilennur mustelinus Lepilennur mustelinus AF474215 AV582631 117 TK125548 Beroboka Lepilennur ruficandatus Lepilennur ruficandatus AF474215 AY582602 143 TK12550 Beroboka Lepilennur ruficandatus Lepilennur ruficandatus AF474217 AY582603 A5 TK12550 Beroboka Lepilennur ruficandatus Lepilennur ruficandatus AF474217 AY582603 A6 TK12550 Tsingy de Bernaraha Lepilennur ruficandatus Lepilennur ruficandatus Lepilennur ruficandatus A7 TK12550 Tsingy de Bernaraha Lepilennur ruficandatus Lepilennur ruficandatus Lepilennur ruficandatus B1 TK12550 Zombitse Lepilennur ruficandatus Lepilennur ruticandatus Lepilennur hubbardi DQ52966 L B15 TK125556 Zombitse Lepilennur ruficandatus Lepilennur hubbardi DQ529373 DQ529666 L B2	ZAH201		Zahamena	Lepilemur mustelims	Lepilemur mustelinus	AF474230	AY582629	AY769429
217 TK125548 Beroboka Lepilemur misselinus Lepilemur ruficandatus Lepilemur ruficandatus Lepilemur ruficandatus AF474215 AY582601 142 TK125549 Beroboka Lepilemur ruficandatus Lepilemur ruficandatus Lepilemur ruficandatus AF474216 AY582602 143 TK12550 Beroboka Lepilemur ruficandatus Lepilemur ruficandatus <td>ZAH216</td> <td></td> <td>Zahamena</td> <td>Lepilemur mustelinus</td> <td>Lepilemur mustelinus</td> <td>AF474231</td> <td>AY582630</td> <td>AY769430</td>	ZAH216		Zahamena	Lepilemur mustelinus	Lepilemur mustelinus	AF474231	AY582630	AY769430
117 TK125548 Beroboka Lepilemur ruficandatus Lepilemur ruficandatus Lepilemur ruficandatus AF474215 AY582601 142 TK125549 Beroboka Lepilemur ruficandatus Lepilemur ruficandatus AF474217 AY582602 A5 TK12550 Tsingy de Bemaraha Lepilemur ruficandatus Lepilemur ruficandatus Lepilemur randriamasoli DQ529371 AY58260 A7 TK12550 Tsingy de Bemaraha Lepilemur ruficandatus Lepilemur randriamasoli DQ529371 DQ529661 1 A8 TK12550 Tsingy de Bemaraha Lepilemur ruficandatus Lepilemur hubbardi DQ529373 DQ529663 1 B8 TK12555 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529374 DQ529665 1 B15 TK125557 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529375 DQ529668 1 B2 TK125557 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529379 DQ529669 1 B2 Zombitse Lepi	ZAH217		Zahamena	Lepilemur mustelinus	Lepilemur mustelinus	AF474232	AY582631	AY769431
142 TK125549 Beroboka Lepilemur ruficandarus Lepilemur ruficandarus Lepilemur ruficandarus Lepilemur ruficandarus Lepilemur ruficandarus AF474217 AY582603 A5 TK125508 Tsingy de Bernaraha Lepilemur ruficandarus	10R117	TK125548	Beroboka	Lepilemur ruficaudatus	Lepilemur ruficandatus	AF474215	AY582601	AY769400
147 TK125550 Beroboka Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur rudicaudatus	IOR142	TK125549	Beroboka	Lepilemur ruficaudatus	Lepilemur ruficaudatus	AF474216	AY582602	AY769401
A5 TKL25508 Tsingy de Bemaraha Lepilemur ruficaudatus Lepilemur randrianasoli DQ529370 DQ529661 A7 TK125509 Tsingy de Bemaraha Lepilemur ruficaudatus Lepilemur randrianasoli DQ529372 DQ529662 B8 Zombitse Lepilemur ruficaudatus Lepilemur ruticaudatus Lepilemur hubbardi DQ529373 DQ529663 B12 TK12555 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529374 DQ529663 B15 TK12555 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529375 DQ529665 B16 TK125557 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529376 DQ529667 B2 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529378 DQ529668 B2 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529378 DQ529669 B2 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 B2 Zombitse Lepilemur ruficaudatus <td< td=""><td>IOR147</td><td>TK125550</td><td>Beroboka</td><td>Lepilemur ruficandatus</td><td>Lepilemur ruficandatus</td><td>AF474217</td><td>AY582603</td><td>AY769402</td></td<>	IOR147	TK125550	Beroboka	Lepilemur ruficandatus	Lepilemur ruficandatus	AF474217	AY582603	AY769402
A7 TK125509 Tsingy de Bemaraha Lepilemur ruficaudatus Lepilemur randriamasoli DQ529371 DQ529661 88 Zombitse Lepilemur ruficaudatus Lepilemur ruticaudatus Lepilemur ruticaudatus Lepilemur hubbardi DQ529373 DQ529663 89 TK125558 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529374 DQ529665 815 TK125556 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529376 DQ529666 816 TK125557 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529666 821 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 822 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 82 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 82 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669	EMA5	TK125508	Tsingy de Bemaraha		Lepilemur randrianasoli	DQ529370	DQ529660	DQ529518
A7 TK125510 Tsingy de Bemaraha Lepilemur ruficaudatus AV582593 AV582593	EMA6	TK125509	Tsingy de Bemaraha		Lepilemur randrianasoli	DQ529371	DQ529661	DQ529519
B8 Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur rubbardi DQ529374 DQ529665 B12 TK125556 Zombitse Lepilemur ruficaudatus Lepilemur rubbardi DQ529375 DQ529665 B16 Lepilemur ruficaudatus Lepilemur ruficaudatus Lepilemur rubbardi DQ529377 DQ529665 B21 Zombitse Lepilemur ruficaudatus Lepilemur rubbardi DQ529378 DQ529669 B22 Zombitse Lepilemur ruficaudatus Lepilemur rubbardi DQ529378 DQ529669 B22 Zombitse Lepilemur ruficaudatus Lepilemur rubbardi DQ529378 DQ529669 B22 Anhanaharibe-Sud Lepilemur ruficaudatus Lepilemur readi AF474198 AY582593	EMA7	TK125510	Tsingy de Bemaraha		Lepilemur randrianasoli	DQ529372	DQ529662	DQ529520
B9 TK125558 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529374 DQ529664 B12 TK125556 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529375 DQ529665 B16 TK125557 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529377 DQ529667 B21 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529378 DQ529669 B32 Zombitse Lepilemur ruficandatus Lepilemur hubbardi DQ529378 DQ529669 B32 TK125523 Anhanaharibe-Sud Lepilemur nustelinus Lepilemur seali AF474198 AY582593	SMB8		Zombitse	Lepilemur ruficaudatus	Lepilemur hubbardi	DQ529373	DQ529663	DQ529521
Harring TK12556 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529375 DQ529665 R15 TK12557 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529377 DQ529667 R20 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529378 DQ529668 R21 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 R32 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 TK125523 Anhanaharibe-Sud Lepilemur nustelinus Lepilemur seali AF474198 AY582593	OMB9	TK125558	Zombitse	Lepilemur ruficaudatus	Lepilemur hubbardi	DQ529374	DQ529664	DQ529522
Help TK12557 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529376 DQ529666 Rel Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529377 DQ529668 Rel Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 TK125523 Anhanaharibe-Sud Lepilemur nustelinus Lepilemur seali AF474198 AY582593	OMB12	TK125556	Zombitse	Lepilemur ruficaudatus	Lepilemur hubbardi	DQ529375	DQ529665	DQ529523
20mbitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529377 DQ529667 20mbitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529378 DQ529668 20mbitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 TK125523 Anhanaharibe-Sud Lepilemur nustelinus Lepilemur seali AF474198 AY582593	OMB15	TK125557	Zombitse	Lepilemur ruficaudatus	Lepilemur hubbardi	DQ529376	DQ529666	DQ529524
20mbitse Lepilemur ruficandatus Lepilemur hubbardi DQ529378 DQ529668 20mbitse Lepilemur ruficandatus Lepilemur hubbardi DQ529379 DQ529669 TK125523 Anhanaharibe-Sud Lepilemur mustelinus Lepilemur seali AF474198 AY582593	OMB16		Zombitse	Lepilemur ruficaudatus	Lepilemur hubbardi	DQ529377	DQ529667	DQ529525
2 Zombitse Lepilemur ruficaudatus Lepilemur hubbardi DQ529379 DQ529669 TK125523 Anhanaharibe-Sud Lepilemur mustelinus Lepilemur seali AF474198 AY582593	OMB21		Zombitse	Lepilemur ruficaudatus	Lepilemur hubbardi	DQ529378	DQ529668	DQ529526
TK125523 Anhanaharibe-Sud Lepilemur mustelinus Lepilemur seali AF474198 AY582593	OMB52		Zombitse	Lepilemur ruficandatus	Lepilemur hubbardi	DQ529379	DQ529669	DQ529527
	.R2	TK125523	Anhanaharibe-Sud	Lepilemur mustelinus	Lepilemır seali	AF474198	AY582593	AY769392

Catalog Number	TK Number	Location	Original Species Designation	Current Species Designation	12s	PAST ^b rRNA ^b	D loop ^b
JAR3	TK125524	Anhanaharibe-Sud	Lepilemur mustelinus	Lepilemur seali	AF474199	AY582594	AY769393
JAR8	TK125525	Anhanaharibe-Sud	Lepilemur mustelinus	Lepilemur seali	AF474200	AY582595	AY769394
JAR3.38		Anhanaharibe-Sud	Lepilemur mustelinus	Lepilemur seali	DQ529352	DQ529642	DQ529500
JAR3.39		Anhanaharibe-Sud	Lepilemur mustelinus	Lepilemur seali	DQ529353	DQ529643	DQ529501
JAR3.46		Anhanaharibe-Sud	Lepilemur mustelinus	Lepilemur seali	DQ529354	DQ529644	DQ529502
NARA4.20		Mananara-Nord	Lepilemur mustelinus	Lepilemur seali	DQ529402	DQ529694	DQ529552
RANO261		(Ivontaka-Sud) Ranomafana	Avahi laniger	Avahi laniger	AF474233	AY582559	AY584496
RANO67		Ranomafana	Avahi laniger	Avahi laniger	AY254047	AY582558	AY584495
ANK33		Ankarafantsika	Avahi occidentalis	Avahi occidentalis	AF474241	AY582560	AY584497
RANO332		Ranomafana	Propithecus edwardsi	Propithecus edwardsi	AF474236	AY582556	AY585739
MOR68		Beroboka	Propithecus verreauxi	Propithecus verreauxi	AF474237	AY582557	AF585739
RANO45		Ranomafana	Eulemur fulvus rufus	Eulemur fulvus rufus	AF474234	AY582561	AY585738
FAN21		Fandriana	Varecua variegata variegata	Varecia variegata variegata	AF474235	AY582555	AY584494
RANO250		Ranomafana	Microcebus rufus	Microcebus rufus	AY582713	AY582546	AY159722
ANK7		Ankarafantsika	Microcebus ravelobensis	Microcebus ravelobensis	AY582712	AY 582545	AY159695
KIAN124		Kianjavato	Hapalemur simus	Hapalemur simus	AF474238	AY582548	AY584488
RANO338		Ranomafana	Hapalemur simus	Hapalemur simus	AY582714	AY582547	AY254049
RAN0351		Ranomafana	Hapalemur aureus	Hapalemur aureus	AF474239	AY582549	AY584489
RAN0352		Ranomafana	Hapalemur aureus	Hapalemur aureus	AY582715	AY582550	AY254048

RANO61	LUCATION	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST⁵	D loop ^b
	Ranomafana	Hapalemur griseus griseus	Hapalemur griseus griseus	AY582716	AY582551	AY584490
RANO62	Ranomafana	Hapalemur griseus griseus	Hapalemur griseus griseus	AY582717	AY582552	AY584491
ANAL2.23	Analamera	Hapalemur griseus occidentalis	Hapalemur griseus occidentalis AY582718	AY582718	AY582554	AY584493
GAR9	Manongarivo	Hapalemur griseus occidentalis	Hapalemur griseus occidentalis	AY582719	AY582553	AY584492
RANO229	Ranomafana	Cheirogaleus major	Cheirogaleus major	AF474240	AY582563	AY254050
GAR8	Manongarivo	Cheirogaleus medius	Cheirogaleus medius	AY192626	AY582562	AY584498

